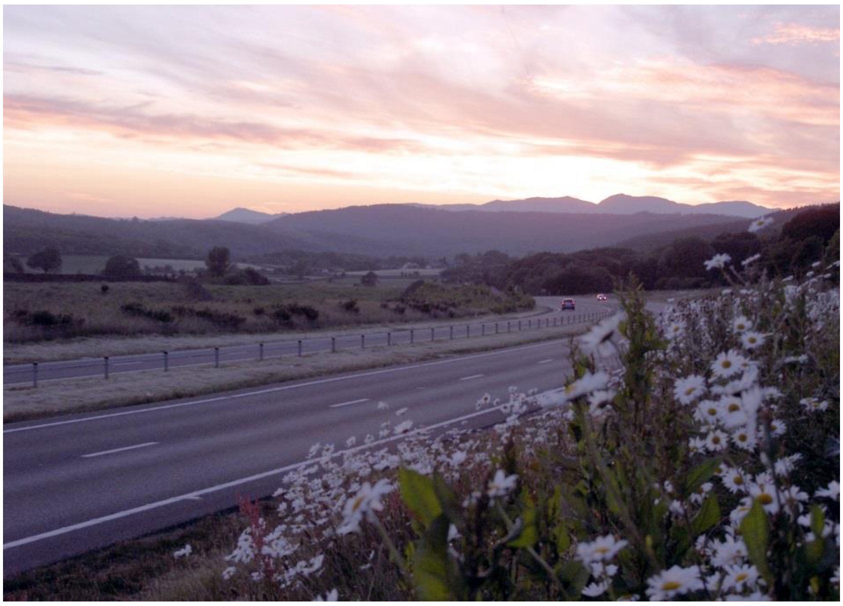
The effect of roads on bats in the UK: a model for evidence based conservation



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The candidate confirms that the work submitted is her own, except where work which has formed part of jointly-authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

Chapters 2 and 5 are based on the following jointly-authored publications:

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In both publications Anna Berthinussen and John Altringham designed the experiments. Anna Berthinussen performed the experiments, analyzed the data and wrote the first draft of the paper. John Altringham and Anna Berthinussen both made edits to later drafts. University of Leeds students assisted with field work and acknowledgements are given where due.

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Abstract

Despite their protected status, little research has been done into the effects of roads on bats or the effectiveness of current mitigation practice. We conducted broadband acoustic surveys on 20 walked transects perpendicular to two major roads in the UK, the M6 in Cumbria, and the M5 in Somerset. Bat activity and habitat variables were recorded at different distances from the road, and the relationship between these variables were investigated using generalised estimated equations (GEE), and ordinal logistic regression. Total bat activity and the activity of *Pipistrellus pipistrellus* (the most abundant species) were positively correlated with distance from both roads, although the magnitude of the effect was greater by the M6. Distance from the road was positively correlated with the number of bat species by the M6 only. Higher quality habitat surrounding the M5 may have reduced the negative road impacts. The use of direct sampling to collect acoustic data revealed a greater road effect than time expansion methods, which is likely due to increased accuracy through continuous sampling and a larger dataset. Three underpasses and four wire bat gantries were investigated in northern England using echolocation call recordings and observations. The bat gantries were ineffective and used by a very small proportion of bats. Only one underpass located on a pre-construction commuting route could be considered to be effective, and attempts to divert bats were unsuccessful. Further research should focus on crossing structures built on original bat commuting routes, such as underpasses and green bridges. We suggest an integrated approach to mitigation, combining crossing structures and habitat improvements. New crossing structures need to be developed and tested, given the poor success of current structures. Robust pre- and post-construction monitoring using a standardised methodology is essential to assess the effectiveness of mitigation schemes and build an evidence-base for successful conservation.

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List of Abbreviations

AONB – Area of Outstanding Natural Beauty

GEE – Generalised Estimating Equations

GIS – Geographic Information System

SAC – Special Area of Conservation

SSSI – Site of Special Scientific Interest

Chapter 1: General Introduction

1.1 Scope

The focus of this research is to investigate the effect of road developments on bats, and the effectiveness of current mitigation measures. This introductory chapter provides an overview of the possible effects of roads on bats, and broadly reviews our current knowledge. Where evidence for bats is lacking, the effects of roads on other wildlife are discussed. The current legislation to protect bats in the UK and the rest of the EC, and the requirements for mitigation are summarised. Existing and potential mitigation methods are explained and evidence for their effectiveness is discussed. Issues relating to the assessment of the effectiveness of mitigation are addressed, and the importance of evidence-based conservation is raised. Lastly, the purpose of this research and the principle aims are presented.

1.2 Bat ecology and conservation

There are over 1,250 bat species distributed across the world, comprising more than a fifth of all known mammal species. Bats are an extremely diverse group of mammals inhabiting a wide variety of habitats, with a unique combination of adaptations including powered flight, echolocation and hibernation. Despite this, there has been a dramatic world-wide decline in bat populations in recent years with approximately a quarter of bat species being globally threatened (Mickleburgh *et al.* 2002). Anthropogenic activities resulting in habitat destruction, degradation and fragmentation are a major threat to bats, as well as hunting, persecution, invasive species and disease, and climate change (Altringham 2011). Bats are particularly vulnerable to disturbance and recover slowly from population crashes due to their life history strategy of low fecundity, longevity and a large landscape ecology (Barclay & Harder 2003). Bats frequently live for 20-30 years, can take several years to reach sexual maturity and usually produce only one pup per year. Bats use large areas of the landscape, and can make long distance commutes between summer roosts and foraging areas and to winter hibernation sites (Senior *et al.* 2005; Rivers *et al.* 2006).

Furthermore, many bat species roost in buildings and forage in suburban environments, bringing them into close contact and often conflict with humans.

1.3 Bats and the law

There are 17 resident species of bat in the UK and all are protected by both UK (The Wildlife and Countryside Act 1981, as amended; The Countryside and Rights Of Way Act 2000; National Environment and Rural Communities (NERC) Act 2006) and EU legislation (The Conservation of Habitats and Species Regulations 2010). Under these laws, all bats are protected from being killed, injured, taken or disturbed and their roosts are protected from damage, destruction or their access being obstructed. Two UK bat species, *Barbastella barbastellus* and *Myotis bechsteinii*, are listed on the IUCN red list as near threatened (IUCN 2012), and all bat species are an important consideration in national and local recovery plans (JNCC and Defra (on behalf of the Four Countries' Biodiversity Group) 2012). It is also a legal requirement that a license is obtained from the appropriate Statutory Nature Conservation Organisation if it is necessary to disturb any species of bat. Developers must demonstrate that they will put in place mitigation measures to minimise the impact and compensate for any loss to bat foraging or roosting habitat (Mitchell-Jones 2004). Similar laws apply to bats in Europe, North America and Australia.

1.4 The effects of roads on vertebrates

Human activity is constantly changing the face of the earth and habitat fragmentation is a major threat to biodiversity (Hambler & Canney 2013). Developments fragment the landscape resulting in small isolated habitat patches surrounded by urban or agricultural land. The species richness of many organisms decreases with fragment area (e.g. Stratford & Stouffer 1999; Ferraz *et al.* 2007; Laurance *et al.* 2011), and smaller fragments are likely to lose species more quickly (Laurance *et al.* 2011; Stouffer *et al.* 2011), although such losses may not be immediately apparent due to an extinction debt (Kuussaari *et al.* 2009; Wearn *et al.* 2012). There can be deleterious effects from the unnatural abrupt edges created by fragmentation with changes in microclimate and the composition of communities (Fischer &

Lindenmayer 2007; Laurance *et al.* 2011). Habitat isolation also reduces landscape connectivity limiting the dispersal of species, and may reduce gene flow resulting in a loss of genetic diversity (e.g. Lindsay *et al.* 2008; Dixo *et al.* 2009). Species vary in their sensitivity to fragmentation, those with large territories or dispersal ranges are most affected (Henle *et al.* 2004), for example, wide-ranging bird and mammal species have been lost rapidly from small fragments of the Amazonian rainforest (Laurance *et al.* 2011).

Road construction is an example of an anthropogenic activity that causes habitat fragmentation. Roads destroy and degrade habitat and dissect the natural landscape (Forman *et al.* 2003). In 2010, the total length of the road network in Great Britain was estimated to be 245,000 miles, with 244 billion vehicle miles of journeys taking place on these roads per year (Department for Transport 2011). Despite huge road length and traffic volumes world-wide, the effects of roads on wildlife had received relatively little attention until the coining of a new scientific discipline by Forman and Alexander (1998) called ‘Road Ecology’. Forman brought to attention the potentially devastating effects of roads on the natural world and the lack of knowledge in this area. Since then, Road Ecology has become increasingly well studied, although there are still relatively few studies of bats.

Reviews of early work concluded that the densities of a range of vertebrates, including birds, are negatively correlated with road density and positively correlated with distance from the road (Trombulak & Frissell 2000; Coffin 2007). However, roads may have a positive effect on some species. There is evidence that roadside verges can provide habitat for small mammal populations, especially in disturbed or hostile landscapes (Bissonette & Rosa 2009; Ruiz-Capillas *et al.* 2013). For example, densities of white-footed mice, *Peromyscus leucopus,* increase in proximity to roads because of the creation of favourable habitats along road verges and a reduction in predators (Rytwinski & Fahrig 2007), but the same species is reluctant to cross roads (McGregor *et al.* 2008). It is likely that positive effects are limited to relatively few generalist species. Also, roadside habitats may act as ecological traps as these populations may suffer increased mortality rates due to collisions with traffic, which could make them unsustainable sinks without immigration from source populations in the surrounding area.

Fahrig & Rytwinski (2009) reviewed 79 studies that between them investigated 131 species (including invertebrates, reptiles, amphibians, birds and mammals) and found that negative road effects outweighed the positive by a factor of five. In a meta-analysis of 49 studies that between them investigated 234 bird and mammal species, the main response (with the exception of some raptor species which were more abundant along roads) was of road avoidance and reduced population densities in proximity to roads (Benítez-López *et al.* 2010). Another meta-analysis study using data from 75 studies and over 300 species (including reptiles, amphibians, birds and mammals) found that species with similar life history traits to those of bats (e.g. low reproductive rates, greater mobility and with larger territories) were more susceptible to the negative impact of roads (Rytwinski & Fahrig 2012).

Possible effects of roads on wildlife include direct mortality from vehicle collisions, habitat destruction, habitat fragmentation and degradation, barrier effects, or disturbance from light, noise and chemical pollution. The magnitude of road effects is likely to vary over time (Balkenhol & Waits 2009) and multiple effects will be cumulative with potentially serious consequences in the long term (Figure 1.1). There may also be far reaching effects, such as the cascading consequences that occur in ecological communities when the abundances of key species are altered (Francis *et al.* 2009).

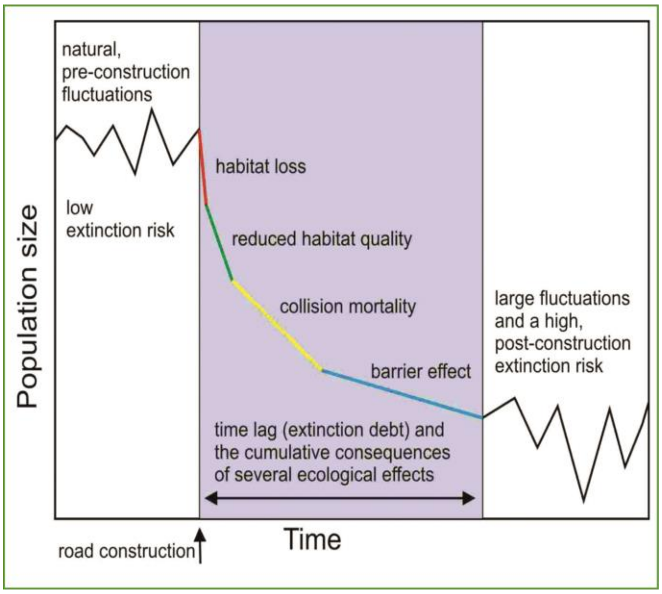

Figure 1.1: Illustration of the cumulative and delayed effect of roads on wildlife populations. Based on Forman *et al.* (2003).

1.4.1 The barrier effect

The barrier effect refers to the restrictions a road may impose on the dispersal of wildlife. Roads create a break in natural habitats introducing unnatural shapes and materials, wide open spaces and altered habitat along road verges (e.g. Figure 1.2).

Figure 1.2: Aerial view of a motorway bisecting woodland.

The M50 motorway in Wales, UK. © 2013 Google Earth © 2013 Getmapping plc.

It is likely that roads will pose a significant barrier to bats due to their dependence on linear elements, such as hedgerows, within the landscape for commuting and navigation (Frey-Ehrenbold *et al.* 2013). Bats commute nightly from their roosts to foraging habitats, and may travel as far as 20 km to feed (Bontadina *et al.* 2002; Senior et al. 2005). Bats also migrate in the autumn to swarming and hibernation sites and travel even greater distances of 60 km or more (Rivers *et al.* 2006). Most species show a high fidelity to specific sites and flight routes over many generations and rely on these linear elements to guide them (Bontadina *et al.* 2005). The continuity of these flight routes is therefore important, and severance by road developments could have devastating consequences. Access to important foraging sites could be cut and may result in the use of suboptimal commuting routes or foraging locations, causing a decrease in fitness. The decrease in ‘accessible habitat’ created by the barrier effect has been shown to have far more serious consequences on a species’ survival than when direct habitat loss is considered alone (Eigenbrod *et al.* 2008). The amount of ‘accessible habitat’ was found to be a strong predictor of anuran species richness in forest habitat bisected by a road, in comparison to direct habitat loss alone which was found to be a poor predictor leading to an underestimation of negative effects.

Motorways can restrict habitat accessibility in female Bechstein's bats, *Myotis bechsteinii*, resulting in smaller foraging areas and reduced reproductive success in proximity to a motorway, indicating a barrier effect (Kerth & Melber 2009). There is also evidence of road avoidance behaviour. Bats have been found to reverse their course when approaching roads that bisect their commuting routes, and even small gaps of less than 5 m in treelines and hedgerows along a flight line will cause bats to change direction and veer away from their commuting routes (Zurcher *et al.* 2010; Bennett & Zurcher 2013). However, it has also been shown that bats will fly close to the ground over open spaces (Russell *et al.* 2009) and some low-flying bat species have been observed attempting to cross wide roads that sever commuting routes along mature hedgerows (Abbott *et al.* 2012a), increasing the risk of collision mortality.

The strength of the barrier effect on bats may also be linked with road width and traffic volume. Bats were found to be twice as likely to veer away from roads that bisect their commuting routes in the presence of traffic (Zurcher *et al.* 2010). Foraging bats have been found to fly regularly over a two lane road with little traffic, but not over a busy four lane motorway (Kerth & Melber 2009), although the effects of road width and traffic volume could not be separated.

Roads that act as barriers to wildlife can also have negative genetic effects by increasing the functional isolation of populations (Holderegger & Di Giulio 2010). There is evidence of this in other wildlife, for example bank voles, *Clethrionomys glareolus*, were found to be genetically different either side of a main four lane highway (Gerlach & Musolf 2000), and roads were found to restrict gene flow in wide-ranging, mobile species such as coyotes, *Canis latrans*, and bobcats, *Lynx rufus* (Riley *et al.* 2006). A recent review found that 35 out of 51 studies showed negative effects of roads on either genetic diversity within or genetic differentiation between populations of animals (including invertebrates, mammals and amphibians), with effects apparent over only a few generations (Holderegger & Di Giulio 2010). There has been no research into the genetic effects of roads on bat populations.

1.4.2 Collision mortality

Collision mortality is an obvious direct effect of roads on wildlife. Estimates of wildlife killed on roads are high, with historic figures such as one million vertebrates per day on roads in the United States (Forman & Alexander 1998).

Bats are certainly vulnerable to collision mortality as they have been found to fly low to the ground when crossing open spaces (Russell *et al.* 2009) placing them in the path of oncoming traffic. Research in Poland shows that up to 6.8 bats/km/year are being killed along stretches of road near Warsaw, with 14 different species affected (Lesinski 2007), and weekly searches of 16.6 km of highway in a National Park between April and October revealed 61 casualties and 7 species (Lesinski *et al.* 2010). In the Czech republic, an 8 km stretch of highway was searched 25 times at weekly intervals from May to October 2007, revealing 119 bat carcasses representing 12 species (Gaisler *et al.* 2009). In Pennsylvania, US, during a 36 day search of several kilometres of highway, 29 road-killed *Myotis* bats were found (Russell *et al.* 2009). These results show that bats *are* being killed along roads, and that a diverse range of species are affected.

However, it is difficult to reliably quantify the number of bats killed on roads, as counts often represent severe underestimates due to searcher efficiency and removal by scavengers, with actual mortality rates potentially being a factor of 12-16 times higher (Slater 2002; Santos *et al.* 2011). Attempts have been made to estimate the effect of collision mortality on roost populations, with corrections applied to account for underestimates. For example, the number of deaths over 5 years on a two-lane major road in the UK was calculated to represent at least 5% of the probable annual recruitment through births to a colony of lesser horseshoe bats in the vicinity (Altringham 2008). However, this is a conservative estimate, with reported figures only doubled to account for corpses not found and scavenged, in comparison to the 12-16 fold increase which has been suggested (Slater 2002). Even a relatively small increase in mortality may have serious consequences for the viability of populations of species with low reproductive rates, such as bats (Forman & Alexander 1998).

Although mortality rates and the subsequent effect on populations are difficult to quantify, studies of bats killed on roads show informative patterns, with spatial aggregation and seasonal variation of road kills, as well as species specific effects. Collision mortality rates of bats have been found to be higher on stretches of road surrounded by high quality habitat such as high canopy cover (Russell *et al.* 2009), wetland habitats (Gaisler *et al.* 2009), forested areas, and where roads cross linear elements used as bat flyways (Lesinski 2007). Rates were lowest in open country or densely built up areas (Lesinski 2007; Russell *et al.* 2009). In Europe, collision mortality rates were also found to be higher in late August and September (Slater 2002; Brinkmann *et al.* 2003; Gaisler *et al.* 2009) and dominated by common and low flying *Pipistrellus* and *Myotis* species. *Nyctalus noctula*, a high flier foraging in open spaces, was found to have the lowest representation in road kills. A high number of young were recorded in the road kills and may account for the seasonal peaks, which occur at a time of year when young bats disperse from the roost (Lesinski 2007). It has been found that young bats fly more slowly (Racey & Swift 1985) and their inexperience when they begin flying may make them more vulnerable to collisions with vehicles. These findings have important implications for conservation and mitigation for identifying high risk locations, species and times of year.

1.4.3 Habitat fragmentation and edge effects

Road construction can result in direct loss of foraging and roosting sites for bats. A six lane motorway (3+3) alone occupies 3 ha of habitat per kilometre, with the addition of service lanes, slip roads, junctions and embankments consuming even more habitat. However, it is not only this direct loss of habitat that has ecological consequences. Roads fragment the landscape, reducing the size of habitat patches and decreasing connectivity between them. Habitat degradation can also occur along the edges of disturbed areas and extend some way into the habitat, with negative consequences on wildlife. This has been described as the ‘road-effect zone’, and may extend several kilometres from the road itself, with asymmetric convoluted boundaries due to spatial patterns of habitats and wildlife (Forman 2000;

Forman & Deblinger 2000). The ecological footprint of a road may also overlap with the effects of neighbouring roads causing an accumulation of road effects in the landscape.

There is a lack of research into the effect of habitat degradation and edge effects caused by roads on the distribution of bats. There are numerous studies showing negative impacts on many other types of wildlife, including birds. A reduction in abundance of insectivorous birds was found up to 2 km from an industrial road in Amazonia (Canaday 1996), the density of breeding bird species in grasslands and woodlands was found to be reduced adjacent to roads in the Netherlands, and the success of yearling males was found to be 50% lower with disturbance distances of up to 3530 m (Reijnen & Foppen 1994; Reijnen *et al.* 1996). A meta-analysis by Benítez-López *et al.* (2010) found that road infrastructures had an effect on bird population densities up to 1 km from roads, and mammal population densities up to 5 km.

1.4.4 Noise pollution

Roads are the most spatially extensive source of anthropogenic noise, and calculations from the US show that 83% of the land area is within 1061 m of a road experiencing traffic noise levels of at least 20 dB, exceeding average levels of ambient low frequency noise in most natural habitats (Barber *et al.* 2009).

Anthropogenic noise is likely to impact wildlife through masking, which inhibits the ability to hear natural sounds (Barber *et al.* 2009). This has implications for communication, hunting efficiency, and the ability to detect predators. Simulated traffic noise has been found to decrease the foraging efficiency of the gleaning greater mouse-eared bat, *Myotis myotis*, with decreased prey capture rates and increased search times during indoor flight room experiments (Schaub *et al.* 2008; Siemers & Schaub 2010). These results suggest that habitats in close proximity to roads may be degraded in their suitability for foraging by passive listening species. These effects could extend up to 60 m from roads and thus affect large areas (Siemers & Schaub 2010). However, noise avoidance behaviour could also confer some benefits for these species, as they would be less likely to come within close proximity to roads, reducing the risk of collision mortality.

Little is known about the effect of traffic noise on bat echolocation. A negative effect on echolocation could reduce the foraging ability of aerial hawking species, and also disrupt successful navigation. The studies above argue against this impairment as no change in flight ability or landing accuracy in the presence of traffic noise was found (Schaub *et al.* 2008). Most anthropogenic noise is below 2 kHz (Francis *et al.* 2009), and as echolocating bats use high frequency calls (typically between 11 and 212 kHz), there is unlikely to be much interference. If traffic noise does contain high frequency components, the effects are likely to be restricted to close proximity to roads as high frequency sounds are attenuated rapidly (Hartley 1989). One study found that aerial hawking bat species turned away from roads more frequently when the noise of approaching vehicles exceeded 88 dB (Bennett & Zurcher 2013). It is suggested that vehicle noise above this level may reduce a bat's ability to detect potential threats nearby, but there is no empirical evidence to support this hypothesis.

The effect of traffic noise has been found to have a negative impact on other wildlife species. For example, a significant negative correlation was found between grassland and woodland breeding bird density and noise load (Reijnen & Foppen 1994; Reijnen *et al.* 1996), and nesting species richness was found to decrease in proximity to noise in woodland birds, leading to different avian community structures (Francis *et al.* 2009). These effects relate to communication rather than navigation or foraging. Bats also emit social calls for intra-specific communication which are of a lower frequency than echolocation calls (Barlow & Jones 1997), and therefore more likely to suffer from interference from traffic noise. However, there is currently no evidence for this.

Some species have also been found to modify the frequency of their calls in the presence of traffic noise. For example, in male great tits, *Parus major*, minimum song frequency is positively correlated with territory background noise (Mockford & Marshall 2009). Brazilian free-tailed bats, *Tadarida brasiliensis*, were found to increase call frequencies in the presence of high frequency noise from chorusing insects (Gillam & McCracken 2007) and digitally generated broadband noise (Tressler & Smotherman 2009). However, there is no evidence relating to road traffic noise.

1.4.5 Light pollution

Many major roads and motorways are lit by artificial lighting at night, and there are currently over 7.5 million streetlights in the UK (Highways Term Maintenance Association 2013). The Government recognises light pollution as a potential source of nuisance in common law and various acts are in place to control it (The Environmental Protection Act 1990; The Clean Neighbourhoods and Environment Act (England and Wales) 2005). However, street lighting is excluded from these acts in England and Wales. Recent provisions enacted in Scotland extend to road lighting (The Public Health etc. (Scotland) Act 2008), but similar amendments have yet to be made in the rest of the UK (RECP 2009). Recently, many county councils in England have implemented programmes to reduce energy bills and carbon emissions by removing, dimming or reducing the hours of operation of streetlights within their areas (e.g. North Yorkshire County Council 2013; Somerset County Council 2013). This has resulted in a total of 3,080 miles of motorways and trunk roads in England becoming completely unlit, and a further 47 miles of motorway with streetlights with limited hours of operation (HighwaysIndustry.Com 2012). The impact of this on bat populations has not been investigated.

Several bat species have been observed foraging under white street lamps. Moths and other insects are attracted to the ultraviolet wavelengths found in white lights (Johnsen *et al.* 2006) and will aggregate around them, creating an abundant foraging opportunity for bats. A study in Sweden found a positive correlation between the number of white streetlamps and bat passes (mainly *Pipistrellus pipistrellus*) (Blake *et al.* 1994). Another study in Sweden also found *P. pipistrellus* feeding around streetlights, as well as *Nyctalus noctula*, *Vespertilio murinus*, and *Eptesicus nilssonii* (Rydell 1992). The gross energy intake of *E. nilssonii* foraging under streetlights was found to be twice as high as in woodland, which shows the profitability of exploiting this resource. However, there are also associated disadvantages. Where street lights are used to line busy roads, this brings bats into close contact with traffic, increasing the likelihood of collision mortality. It may also make bats more vulnerable to predation, for example, diurnal raptors such as kestrels have been observed hunting under artificial light along motorways (Jones 2000).

Lighting along roads may also have more complex effects by changing community structures. Research shows that it is only the faster flying species that are able to take advantage of foraging under streetlights (Jones 2000; Brinkmann *et al.* 2003; Downs *et al.* 2003). An increase in *P. pipistrellus* and a decline in *Rhinolophus hipposideros* have been observed throughout Western Europe. Further research into the changes in abundance of these species showed that artificial lighting may be having an effect on bat population dynamics through diffuse exploitative competition (Arlettaz *et al.* 2000). The aggregation of insects around streetlights was found to be causing a deficit of prey in surrounding areas, and as *P. pipistrellus* are able to exploit this resource and *R. hipposideros* are not, this causes the divergent changes in abundance of these species.

There are other negative effects associated with artificial light pollution. The intensity of artificial lighting has been found to affect the emergence time of *Pipistrellus pygmaeus*, with bats emerging later in the presence of white light treatments (Downs *et al.* 2003). Later emergence times reduce the amount of nightly foraging time available, and therefore impact the energy intake and fitness of bats within the roost. Commuting behaviour has also been found to be negatively affected by artificial lighting. Illumination of varying intensity along commuting routes of lesser horseshoe bats, *R. hipposideros,* reduced bat activity dramatically and delayed commuting behaviour, with no evidence of habituation (Stone *et al.* 2009; Stone *et al.* 2012). This has important implications for flight routes in proximity to or crossing roads. Bats were found to avoid lit areas, some even turning around and using alternative routes. These alternative routes may be suboptimal, reduced in quality or longer in distance, increasing energetic demands. This can have consequences for reproductive fitness. Increased commuting distances to foraging areas by lactating female *Myotis grisescens* were found to suppress juvenile growth rates (Tuttle 1976).

1.4.6 Other effects

Road developments may also disrupt local hydrology and polluted run-off may degrade wetland foraging habitats (Hellawell 1988; Highways Agency 2001). A decline in river water quality has been found to reduce both total bat activity and foraging activity of *P. pipistrellus* (Vaughan *et al.* 1996). Other possible effects could include a microclimate effect with roadsides being generally windier, hotter, drier and dustier (Coffin 2007); and negative effects on nearby vegetation and insect populations caused by chemical pollution. A study on automobile exhaust gases showed an associated decline in arthropod diversity and abundance in proximity to a road (Przybylski 1979), and the species composition of vegetation in heathland was found to be altered up to 200 m from a dual carriageway road in the UK (Angold 1997).

1.5 Mitigation

In the UK, the law requires that developers assess the impact of projects on the environment, and mitigate against this impact as part of the development plan (The Town & Country Planning Regulations, 1999). A licence must be obtained for developments that may disturb protected species, such as bats. These are issued by Statutory Nature Conservation Organisations (e.g. Natural England, Countryside Council for Wales, Scottish Natural Heritage) and applicants must show that the proposed scheme results from a genuine need, that there are no satisfactory alternatives and that there will be no adverse effect on the favourable conservation status of the protected species, with adequate mitigation measures implemented to negate or compensate for any such effects (Natural England, 2013). The official definition of a 'favourable conservation status' is that populations of the protected species must be maintained with a large enough area of habitat available to do so in the long term, and with no reduction in the natural range of the species (Council Directive 92/43/EEC). Similar laws requiring permits and mitigation operate throughout Europe, North America and Australia.

There are several different mitigation techniques which are currently being used or have been proposed for bats along road developments, although evidence for their effectiveness is lacking. Most structures aim to guide bats either safely over or under roads, reducing the risk of collision mortality and increasing road permeability to maintain connectivity across the landscape.

1.5.1 Underpasses

Underpasses are tunnels, bridges or culverts that pass beneath the road. Studies have shown that bats will use underpasses to commute (e.g. Bach *et al.* 2004; Kerth & Melber 2009; Boonman 2011; Abbott *et al.* 2012a). However, occasional use by an unknown proportion of individual bats does not guarantee safe crossing routes and continued habitat accessibility for bat populations as a whole. A recent study in Germany found that although seven bat species used three underpasses along a stretch of motorway, *M. bechsteinii* rarely used them and suffered a subsequent reduction in home range size (Kerth & Melber 2009). A study in Ireland found more bats flying through a large underpass than over the road above, but nearly 20% of the most abundant species (*Pipistrellus* spp.) flew directly over the road at risk of collision with traffic (Abbott *et al.* 2012b).

1.5.2 Overpasses

Overpasses are structures that bridge the road, and are designed to guide bats safely across, above the height of traffic. These may be bridges carrying footpaths or minor roads, bat gantries, or green bridges. A study of bat activity at overpasses carrying minor roads over a motorway in Ireland found that 50% of bats crossed over the road below in the path of traffic, rather than over the bridge, and overpasses were used less often than underpasses (Abbott *et al.* 2012a). Bat gantries usually consist of netting or a set of wires spanning the road and are designed specifically for bats. They are presumed to act as linear features that will guide echolocating bats across roads, above traffic height. However, there is no evidence to support their effectiveness. Green bridges are typically wider than other types of overpass and are covered in vegetation, usually planted with hedgerows and trees. A study in Germany found ten bat species using eight green bridges (designed primarily for larger mammals such as deer) to fly over a road (Bach & Muller-Steiss 2005) but the proportions of bats using them are not given, and their effectiveness in maintaining bat populations was not assessed.

1.5.3 Linear elements

It is important to identify and maintain linear elements within the landscape which bats use for commuting and migration. A study investigating the use of alternative routes found that very few bats from a colony would readily use an artificial hedge to commute (Bontadina *et al.* 2005), therefore highlighting the need to maintain existing routes and associated structures. It has also been suggested that overhanging high canopy cover which bridges the road gap (a 'hop-over') either side of roads at potential bat crossing points could maintain commuting routes and facilitate safe crossing (Limpens *et al.* 2005). While there is evidence that bats will cross roads at greater heights in the presence of high canopy cover (Russell *et al.* 2009), the effectiveness of such 'hop-overs' have yet to be assessed.

1.5.4 Other possible measures

Fencing has been suggested to guide bats up and over roads at a safe height (Brinkmann *et al.* 2003). However, the installation of mitigation fencing on the A487 in Wales was found to fail in preventing bats from crossing the road (Billington 2002). Lighting has been suggested to deter bats. Horseshoe bats (*Rhinolophus* spp.) and long-eared bats (*Plecotus* spp.) avoid bright lights so creating unlit stretches of road at safe crossing points could remove the barrier effect for these species and decrease collision mortality (Outen 2002; Stone *et al.* 2009; Stone *et al.* 2012). However, other bat species have been found to be attracted to street lights to forage putting them at risk of collisions with vehicles (Rydell 1992; Blake *et al.* 1994). Traffic measures such as speed limits and warning signs are used to mitigate effects on other wildlife (Glista *et al.* 2009). However, no evidence exists for the use of such measures in the UK and effectiveness is unlikely due to the visibility and small size of bats which are likely to be killed or injured by vehicles even at slow speeds. Ecological compensation has also been suggested to mitigate the impact of roads, for example by directly replacing lost habitat or upgrading the quality of existing habitat, but empirical evidence for the subsequent effects on wildlife is lacking (e.g. Cuperus *et al.* 1999; Rundcrantz 2006; Villarroya & Puig 2013).

1.6 The need for evidence-based conservation

There are multiple effects that roads are and could be having on bats, with potentially negative impacts leading to a reduction in population sizes. Although roads are recognised as a threat to bats and mitigation structures are being installed along road developments, their effectiveness for conserving bats at the population level has not yet been proven. Much of the previous work done on mitigation structures has been through ecological consultancy where environmental survey and monitoring rarely make use of the scientific method. Monitoring is typically short-term and of insufficient duration to draw reliable conclusions, and practices are often based on unverifiable 'knowledge', 'judgement' and 'expertise'. Thus, the effects of developments and the effectiveness of mitigation are rarely assessed objectively or quantitatively. Also, the 'use' of a mitigation structure is often equated to effectiveness. However, it has been shown that 'use' by individuals does not guarantee the survival of the whole population (Corlatti *et al.* 2009) or equate to conservation gain (Van Der Ree *et al.* 2006). Roads are therefore being built with costly mitigation 'solutions' in place that have no evidence to support their effectiveness, leaving bat populations at risk of further decline. There is a pressing need for a change from so called 'expert knowledge'-based conservation and mitigation to a more scientific 'evidence'-based approach if conservation is to be both effective and cost-effective.

As bats are vulnerable to disturbance, are heavily protected by legislation and are often contentious components of large-scale development plans, they make an ideal model with which to examine and improve current approaches. However these issues are applicable to all wildlife, with poor monitoring of mitigation schemes and insufficient evidence for effective conservation being common (e.g. Van der Ree *et al.* 2007; Lesbarrères & Fahrig 2012; Soanes *et al.* 2013).

1.7 Purpose of research

Bat populations are under increasing threat from anthropogenic disturbance such as road developments. Despite, their protected status there has been relatively little research into the effect of roads on bats, and how best to mitigate against negative effects for successful conservation. To date, studies into the effectiveness of mitigation measures have often been subjective and qualitative with inconclusive results. There is an urgent need for further research and for an improvement to current approaches and methods. This project was designed to address the following issues:

(i) To develop a robust and effective method to test the landscape-scale effect of roads on bat populations

(ii) To assess the impact of road developments on the activity and diversity of bat populations using the above approach

(iii) To assess the effectiveness of mitigation structures which are currently being implemented for bats, and explore alternative mitigation options

(iv) To use the collected evidence to provide guidelines and practical advice for future mitigation projects

(v) To demonstrate the value of an evidence-based approach to conservation, and make recommendations for future research

1.8 Thesis outline

Chapter 2 describes the methods developed to test the landscape-scale effect of roads on bat populations, and applies these methods to a two-year field study to assess the impact of a motorway in Cumbria, northern England, on local bat populations. The effects on bat activity and diversity are investigated, and the underlying mechanisms are discussed. Chapter 3 further develops the above methods and applies them to a study on a second motorway in Somerset, south-west England. The effects on bat activity and diversity are explored again, along with the impact of improved habitat quality around roads. Chapter 4 compares two different methods of acoustic data collection used in the study in Chapter 3, and makes recommendations for the most efficient and productive methods to record bat activity and detect road effects on bats. In Chapter 5, the effectiveness of two types of mitigation structure (wire bat gantries and underpasses) are tested. The success of these structures in guiding bats safely over or under roads is investigated in a field study on four bat gantries and three underpasses in northern England. Chapter 6 discusses the implications of our findings for bat conservation, and provides practical guidelines for mitigation and recommendations for future research.

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Chapter 2: The effect of a major road on bat activity and diversity

2.1 Abstract

It is well known that roads can have a significant impact, usually negative, on species and ecosystems. However, despite their protected status in many countries, little research has been done into the effects of roads on bats. With a view to making more informed management recommendations we address the simple question: are bat activity and diversity (as measured with ultrasonic detectors) correlated with distance from a major road? Broadband acoustic surveys were conducted on 20 walked transects perpendicular to the M6, a major road in Cumbria, UK, with bat activity recorded at eight spot checks per transect at different distances from the road. Climatic and habitat variables were also recorded, and the relationships between bat activity and these variables were investigated using generalised estimated equations (GEE), and ordinal logistic regression. Total bat activity, the number of species and the activity of *Pipistrellus pipistrellus* (the most abundant species), were all positively correlated with distance from the road. Total activity was predicted to increase more than three-fold between 0 and 1,600 m from the road, and *P. pipistrellus* activity more than two-fold. These effects were found to be consistent over 2 years. This study is one of the first to show that roads have a major negative impact on bat foraging activity and diversity and is broadly applicable to insectivorous bat communities worldwide. The results highlight the need for bats to be considered seriously in the planning, construction and long term management of road developments, and the need for further research to inform mitigation practice and promote conservation.

2.2 Introduction

Roads fragment the landscape and cause habitat destruction and pollution. Road ecology has become increasingly well studied (e.g. Frair *et al.* 2008; McGregor *et al.* 2008; Halfwerk *et al.* 2011; Summers *et al.* 2011), but most of the literature has focused on terrestrial mammals, amphibians and birds, with relatively few studies of bats. The negative effects of roads on wildlife far outweigh positive effects (e.g. Fahrig & Rytwinski 2009; Benítez-López *et al.* 2010), and the density and diversity of a range of vertebrates, including birds (e.g. Canaday 1996; Summers *et al.* 2011), have been found to be positively correlated with distance from roads.

It is likely that bats are particularly vulnerable to road developments and will be slow to recover from disturbance due to their life history strategy of low fecundity, their longevity and their use of large areas of the landscape (Altringham 2011). Roads may affect bats in three principle ways: (1) kill by collision with vehicles, (2) damage or degrade roosts and foraging areas, and (3) sever critical flight routes used for commuting and migration. Several studies show that bats of many species are killed by collision with vehicles (Lesinski 2007; Gaisler *et al.* 2009; Russell *et al.* 2009; Lesinski *et al.* 2010), although mortality in many of these studies is probably severely underestimated (Slater 2002; Santos *et al.* 2011). Kerth & Melber (2009) found that a major road in Germany restricted habitat accessibility in female Bechstein's bats *Myotis bechsteinii* resulting in smaller foraging areas and reduced reproductive success. Noise pollution from traffic reduced foraging efficiency of *Myotis myotis*, a species that forages by passive listening (Schaub *et al.* 2008; Siemers & Schaub 2010) and Stone *et al*. (2009; 2012) have shown that street lighting is a major deterrent to foraging and commuting lesser horseshoe bats *Rhinolophus hipposideros*. Zurcher *et al*. (2010) and Bennett and Zurcher (2013) found evidence for road avoidance behaviour: bats approaching a road bisecting a commuting route were found to reverse their course more frequently in the presence of traffic.

These studies, and inference from studies of bats described later, suggest that roads are likely to have significant negative impacts on bats, leading to a reduction in population sizes. Bat populations have declined dramatically in the last century in the UK (Harris *et al.* 1995) and in many other countries, leading to increasingly strong legal protection. To satisfy legal requirements, costly mitigation measures are employed on road developments throughout Europe to reduce their impact on bats. However, there is little satisfactory evidence to support their effectiveness (e.g. Altringham 2008) and we have little knowledge of just how much roads do affect bats. This study is a step towards a more evidence-based approach to the bat-road issue. We ask the simple question: are bat activity and diversity (as measured with ultrasonic detectors) correlated with distance from a major road? We show that roads do affect bat activity, suggest what mechanisms underlie the effect and discuss appropriate mitigation and monitoring strategies.

2.3 Methods

2.3.1 Survey Design

Acoustic surveys were conducted on walked transects approximately perpendicular to the M6, a major road in Cumbria, UK (Figure 2.1), between June and September in 2009 and 2010.

Figure 2.1: Photograph of the M6 motorway, Cumbria, UK.
Looking north towards Whinfell Beacon.

Ten unreplicated transects were walked in 2009 and in 2010 (with the addition of ten new transect routes) 20 transects were completed, each walked twice (Figure 2.2). The section studied consists of an 80 km stretch of road. The M6 (which runs from the middle of England to the Scottish border) is a well-established road, completed in 1971. It is a six-lane highway with a central reservation and a total width of 35 m or more. The maximum speed limit is 110 km h^{-1} and the traffic volume on rural sections in Cumbria is 30 - 40,000 vehicles per day (Average Annual Daily Traffic, Cumbria County Council 2011). The M6 is predominantly unlit in Cumbria with the exception of interchanges, junctions and urbanised areas, and all transects were conducted along unlit sections.

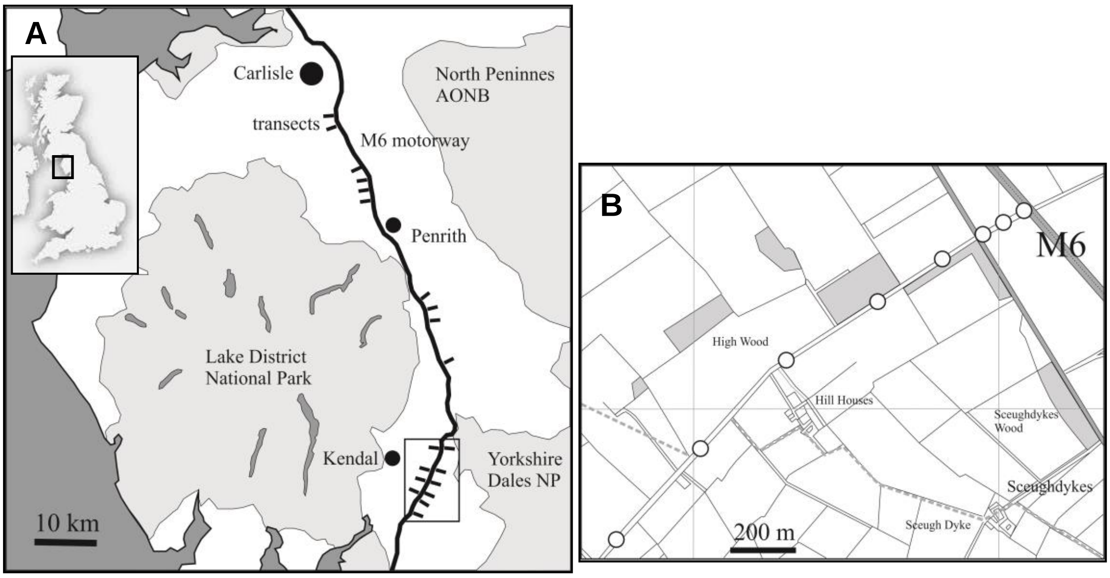

Figure 2.2: Map of the study area and transect routes.

A) The M6 in Cumbria, UK, with transect routes (black markers). Boxed markers indicate transects used in 2009, all transects were used in 2010 (dark grey = Irish Sea, light grey = protected areas: NP (National Park) / AONB (Area of Outstanding Natural Beauty). B) An example of a transect route with spot checks marked (circles), (white areas = open fields, light grey areas = woodland). © *Crown Copyright/database right 2010. An Ordnance Survey/EDINA supplied service.*

Bat activity was recorded for 10 min at each of eight spot checks along each transect at 0, 50, 100, 200, 400, 800, 1,200 and 1,600 m perpendicular to the road. This sampling regime was designed to detect even an effect restricted to the immediate vicinity of the road. Transects were selected using Ordnance Survey maps and site visits to assess their suitability. They were located either side of the road along minor roads or footpaths, through relatively homogenous habitat (avoiding large areas of woodland, water and human habitation) consisting of rural, undulating lowland used predominately for agricultural grazing. Spot check locations were measured and marked using online mapping tools (EDINA, www.edina.ac.uk.) and (in the absence of suitable landmarks) a handheld GPS device (Garmin GPS 60Cx, www.garmin.com) to an accuracy of ± 10 m or better.

Bat echolocation calls were automatically (high gain) detected using a Pettersson D240x broadband bat detector (www.batsound.com), with 100 ms time expanded (to 1 s) calls recorded directly to a solid state recorder (Edirol R-09HR, www.edirol.com) in mp3 (320 kbps) format to reduce file size for storage. One to three calls were captured in each 100 ms recorded segment, sufficient for identification. Each transect commenced 30 minutes after sunset to allow for varying emergence times of different species and was completed two hours after sunset. To account for variation in activity patterns with time, in 2009 five transects were walked toward the road and five away from the road. In 2010 all transects were walked in each direction (away from and towards the road) on separate nights. Transects were only completed in favourable weather conditions, avoiding wet, windy (> 20 km/h) or cold (< 7°C) nights.

Temperature, wind speed, percentage cloud cover and altitude were also recorded at each spot check using a digital anemometer/thermometer (Techno line EA-3010, www.technoline.eu) and GPS. Although transect routes were selected for their habitat homogeneity, the rich mosaic of habitats in the area meant that variation was still present. Habitat types were therefore recorded and classified into 5 categories (Table 2.1).

Table 2.1: The criteria used to classify spot check habitat types.

Grade	Habitat type
1	Fence or wall lining road/path & open fields beyond
2	Hedges/shrubby verges lining road/path & open fields beyond
3	Intermittent medium trees/bushes lining road/path & open fields beyond
4	Intermittent tall trees lining road/path & open fields beyond
5	Continuous tall tree cover lining road/path with woodland &/or open fields beyond

Traffic noise was measured at each spot check by recording for one minute directly onto an Edirol recorder with a sample rate of 48 kHz. Siemers & Schaub (2010) have shown that autobahn traffic noise > 25 kHz is negligible greater than 25 m from the road. Noise recordings were later analysed using GoldWave (www.goldwave.com) digital audio editing software (www.goldwave.com) to produce an RMS (root mean square) level for each recording. This was then converted into decibels and the relative loudness of recordings was compared.

2.3.2 Acoustic analysis

Analysis of echolocation calls was carried out using Batsound Pro software (www.batsound.com). The mp3 files were converted to WAV format using Goldwave. Bat species were identified from the sonograms of their calls using call shape, end frequency and the maximum energy frequency or 'F_{maxe}' (Parsons & Jones 2000). In most cases bats of the genera *Myotis* and *Nyctalus* could not be identified to the species level due to similarity in call structure (Parsons & Jones 2000), and were therefore recorded to the genus level only. We know from capture data of our own and other researchers (e.g. Bellamy *et al.* 2013) that *Myotis nattereri, M. mystacinus* and *M. brandtii* are widespread in the area and likely to be in our *Myotis* group. *M. daubentonii* is also present in the area, but unlikely to have been recorded on our transects since it is confined almost exclusively to water courses. *Nyctalus noctula* is widespread but *N. leisleri* is rare, so most recordings were probably *N. noctula*. A small number of *Pipistrellus* calls (7%) were classified only to genus level, due to the overlap of call parameters of *P. pipistrellus* and *P. pygmaeus*. *Plecotus auritus* is also known to be present in the area, but will be under-recorded due to its low intensity echolocation call and too few recordings were made for meaningful analysis for this species. The number of 'bat passes' was used as a measure of bat activity. A single bat pass was defined as one or more clearly recognisable echolocation call from a single species, separated from the next pass by a gap of at least one second. Measuring bat activity provides a good surrogate for bat density in the study area due to the fidelity of bat colonies to roosting and foraging sites (e.g. Senior *et al.* 2005).

2.3.3 Statistical analysis

A multiple regression model was built to investigate the relationship between bat activity and distance from the road, and at the same time examine the effects of other variables (time, habitat and climate) that could influence bat activity and hence the relationship. This was performed by fitting appropriate generalised estimating equations (GEE) using the *geeglm* function from the library *geepack* (Halekoh *et al.* 2006) in the R program, version 2.12.1 (R Development Core Team 2006). This approach was used to account for within cluster correlation which violates the independence assumption in conventional regression analyses and leads to type 1 errors. GEE's adjust regression coefficients and variance to account for spatially and temporally correlated data, common in ecological research. In this study, a first order autoregressive model AR(1) was used to account for auto-correlation between spot checks conducted along the same route and on the same night. Transect routes were assumed to be independent. The jackknife estimation principle was used to avoid bias due to a small number of clusters (<30). The number of total bat passes were transformed to a log(count+1) to account for the presence of zero counts and large variations in activity observed between transect routes that resulted in heterogeneity. A Gaussian distribution with an identity link was used which gave the best fit to the data. Explanatory variables used in the model were distance from the road, time after sunset, and habitat type. All two-way interactions were not significant and were excluded in the model selection process. Climatic variables were excluded from the analysis as variation was found to be significantly greater between nights and across the season than within nights so were accounted for by modelling the nightly variation in the dependence structure. Noise measurements were also excluded as these were considered irrelevant due to their short operating range. Backward selection and Wald χ^2 tests were used to assess the overall significance of variables and produce the minimum adequate model. Plots of residuals were examined to check for normality and assess the appropriateness of the fitted model. The low abundance of most individual species or genera in this study does not allow for species-specific analysis, except for that of *P. pipistrellus*, for which the above model was repeated.

For the number of bat species/genera groups, a proportional odds ordinal logistic regression was performed using the *lrm* function from the library *Design* in the R program (Harrell 2009). The four identifiable groups of species/genera were treated as ordinal categorical variables defined as 1 (0 species/genera), 2 (1 species/genus), 3 (2 species/genera) and 4 (3 or 4 species/genera). A robust Huber-White "sandwich" covariance estimator (Huber 1967) was applied using the R function *robcov* to correct for auto-correlation due to clustered samples (Harrell 2006), with clusters defined as in the GEE above. Explanatory variables were input as above and Wald χ^2 tests used for model selection. Appropriate graphical methods and statistical tests (χ^2 Test of Parallel Lines) were used to ensure model assumptions were met (Harrell 2006).

The results for the 2010 study are presented below and are supplemented by those from 2009 where appropriate to show the consistency observed over the two years of study. The less intensive study in 2009 was carried out to determine whether a more rigorous investigation in 2010 was justified.

2.4 Results

2.4.1 Overall effects

A total of 3,407 bat passes were recorded during the 2010 study. The significant variables in the GEE minimum adequate model for the transformed number of all bat passes were distance from the road, time after sunset and habitat type (Figure 2.3, Table 2.2). Distance from the road was found to have a significant positive effect on the number of bat passes ($\chi^2 = 19.26$, d.f. = 1, $P < 0.0001$), as was habitat type, ($\chi^2 = 22.5$, d.f. = 4, $P < 0.001$). The results of the model show that there was a significant difference in bat passes between habitat type 1 and types 4 and 5 (Table 2.2). Time after sunset was found to have a significant negative effect on the number of bat passes ($\chi^2 = 5.4$, d.f. = 1, $P < 0.05$). In the 2009 study, 816 bat passes were recorded and similar results were obtained from the GEE modelling with almost identical coefficient estimates (Table 2.2), although habitat type was not found to be significant during the model selection process.

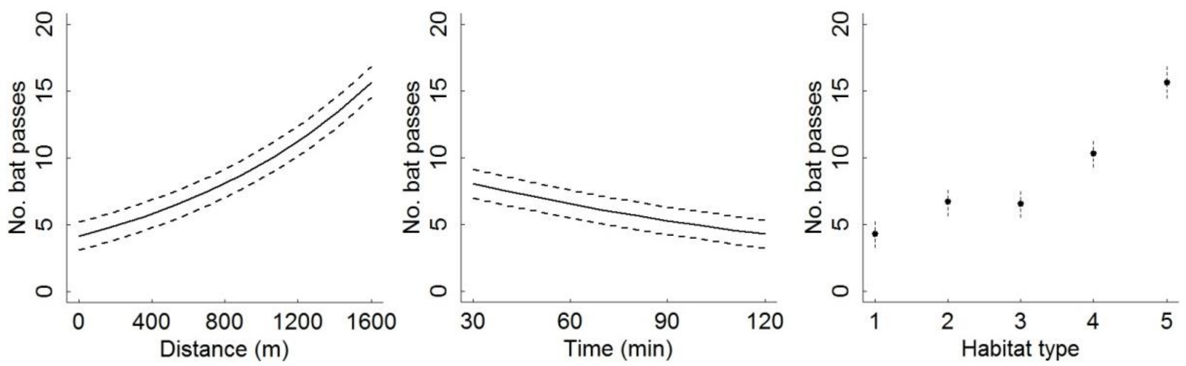

Figure 2.3: Independent effects of each significant variable on total bat activity as predicted by the minimum adequate GEE model.

From left to right: distance from the road, time after sunset (during the 1.5 hour transect) and habitat type (as graded, 1 = low quality, 5 = high quality). Other variables are held constant. Dashed lines indicate approximate 95% confidence intervals.

Table 2.2: Results from the GEE analysis for total bat activity.

Modelling log (1 + number of bat passes) as a function of distance from the road (m), time after sunset (min) and habitat type. All habitat analyses are in comparison with the habitat grade 1 as a reference point.

	2010		2009	
	Bat passes (all species)		Bat passes (all species)	
Coefficients	Estimate	SE	Estimate	SE
Intercept	1.3526 ***	0.26689	2.4812	0.27911
Distance (m)	0.0008 ***	0.00017	0.0008***	0.00019
Time (min)	-0.0070*	0.00286	-0.0128***	0.00315
Habitat 2	0.4438	0.34835	-	-
Habitat 3	0.4215	0.21509	-	-
Habitat 4	0.8739***	0.22473	-	-
Habitat 5	1.2909***	0.33072	-	-
Correlation parameter	0.238	0.0857	0.0109	0.0704
Scale parameter	1.63	0.140	1.08	0.054

** P < 0.05, *** P < 0.001*

Although habitat type varied with distance from the road there was not a simple relationship of increasing habitat ‘quality’ with distance (See Table 2.3). The preferred habitat, grade 5, was actually found to be more frequent in proximity to the road, whereas the least favourable habitats, grades 1 and 2, were found to be more frequent at spot checks away from the road, showing that variation in habitat, as assessed, did not bias the results.

Table 2.3: The number of spot checks found to contain each habitat type.

As graded in this study, at each distance from the road.

Habitat grade	Distance (m)							
	0	50	100	200	400	800	1200	1600
1	5	5	7	12	8	12	8	8
2	2	2	3	6	2	4	6	10
3	14	14	18	10	8	8	12	16
4	13	13	6	10	20	16	12	6
5	6	6	6	2	2	0	2	0

Although bat activity was negatively correlated with time after sunset and positively correlated with habitat type, the effect of distance from the road was constant throughout the night and across different habitat types, with an approximate three-fold increase in the number of bat passes between 0 and 1,600 m from the road, when other significant variables were held constant (Figure 2.4).

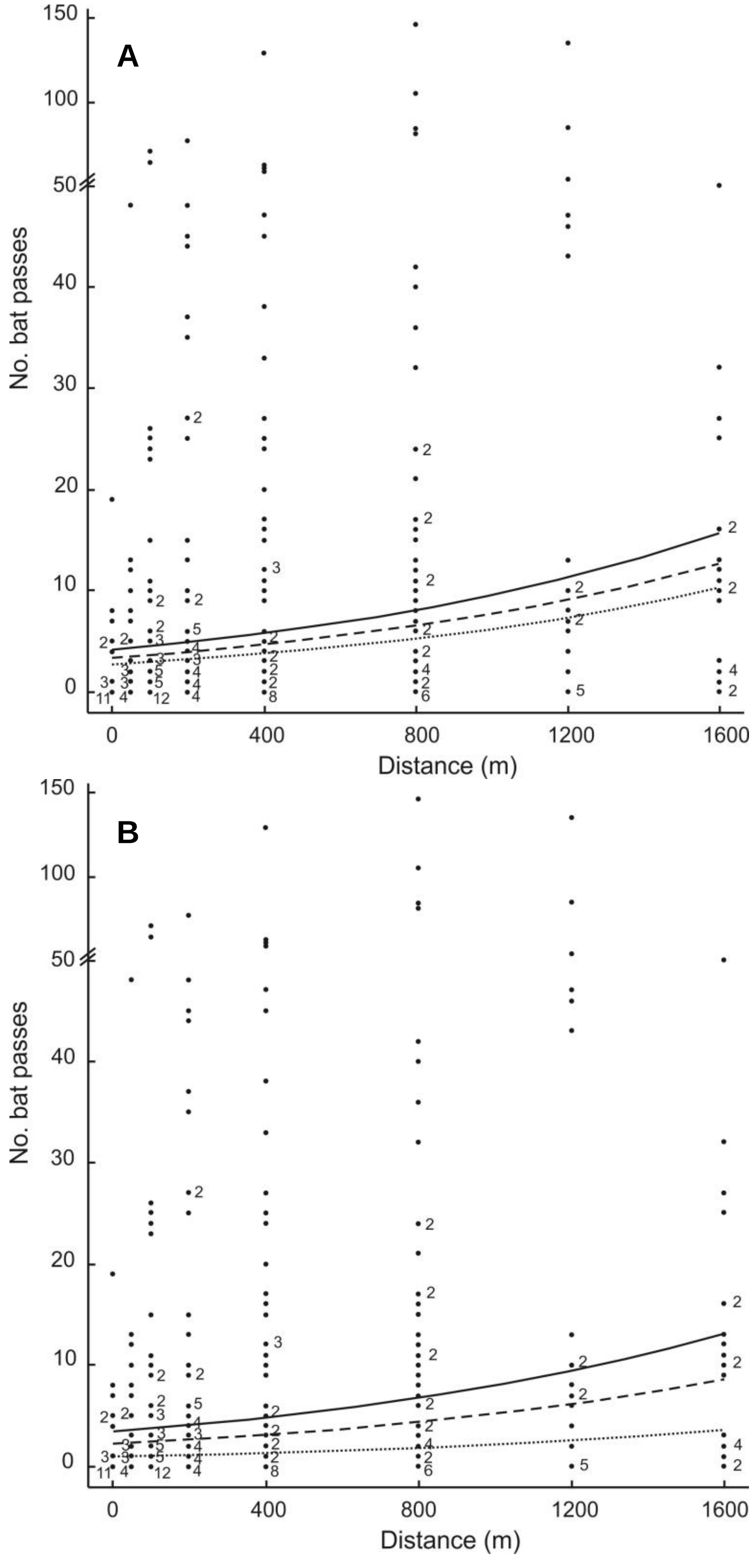

Figure 2.4: GEE model predictions.

A) The effect of distance on the number of bat passes at varying times after sunset, with habitat type held constant at grade 5 (solid line = 30 min, dashed line = 60 min, dotted line = 90 min). B) The effect of distance on the number of bat passes for different habitat types, with time held constant at 55 minutes after sunset, (solid line = habitat grade 5, dashed line = habitat grade 4, dotted line = habitat grade 1). Note the change in y axis scale at 50. Numbers indicate number of replicate points.

2.4.2 Species-specific effects

The species/genera detected during the study were *Pipistrellus pipistrellus, Pipistrellus pygmaeus, Nyctalus* and *Myotis*. *P. pipistrellus* was the most abundant species making up 47% (n = 1607) of the total bat passes, followed by *Myotis* species (16%, n = 560), *Pipistrellus pygmaeus* (14%, n = 483), *Nyctalus* species (14%, n = 470) and unidentified *Pipistrellus* species (7%, n = 247).

The only species found to be abundant enough for statistical analysis was *P. pipistrellus*. The results of the GEE minimum adequate model for the transformed number of *P. pipistrellus* passes reflect the results of the model for all bat passes, with the exclusion of time after sunset as a significant variable (Figure 2.5, Table 2.4). The number of passes increased with distance from the road (χ^2 = 19.26, d.f. = 1, P < 0.0001) and habitat type (χ^2 = 10.4, d.f. = 1, P < 0.01).

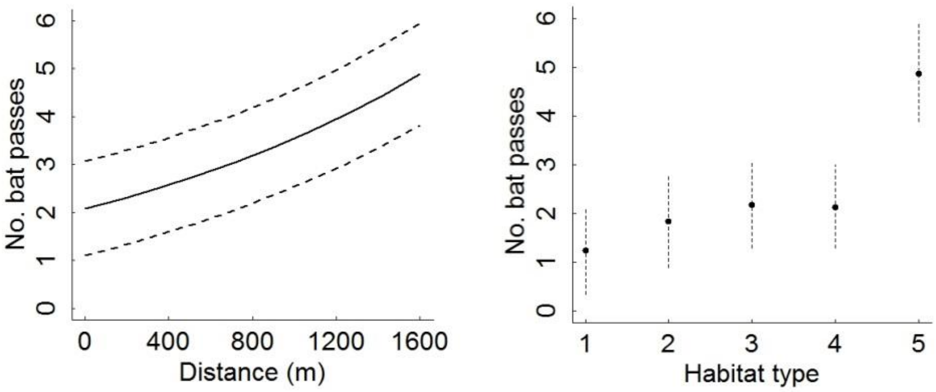

Figure 2.5: Independent effects of each significant variable on *Pipistrellus pipistrellus* activity as predicted by the minimum adequate GEE model.

Left: distance from the road. Right: habitat type (as graded, 1 = low quality, 5 = high quality). Other variables are held constant. Dashed lines indicate approximate 95% confidence intervals.

Table 2.4: Results from the GEE analysis for *Pipistrellus pipistrellus.*

Modelling log (1 + number *Pipistrellus pipistrellus*) as a function of distance from the road (m), time after sunset (min) and habitat type. The habitat analysis is in comparison with the habitat grade 1 as a reference point.

	2010	
	P. pipistrellus passes	
Coefficients	Estimate	SE
Intercept	0.3706**	0.13669
Distance (m)	0.0005***	0.00015
Time (min)	-	-
Habitat 2	0.3941	0.30486
Habitat 3	0.5626**	0.18616
Habitat 4	0.5399***	0.16067
Habitat 5	1.3643***	0.35017
Correlation parameter	0.246	0.0806
Scale parameter	1.37	0.119

*** P < 0.01, *** P < 0.001*

Although statistical analyses were not possible for the other individual species or genera the trend appears to be for an increased number of bat passes with distance from the road (Figure 2.6).

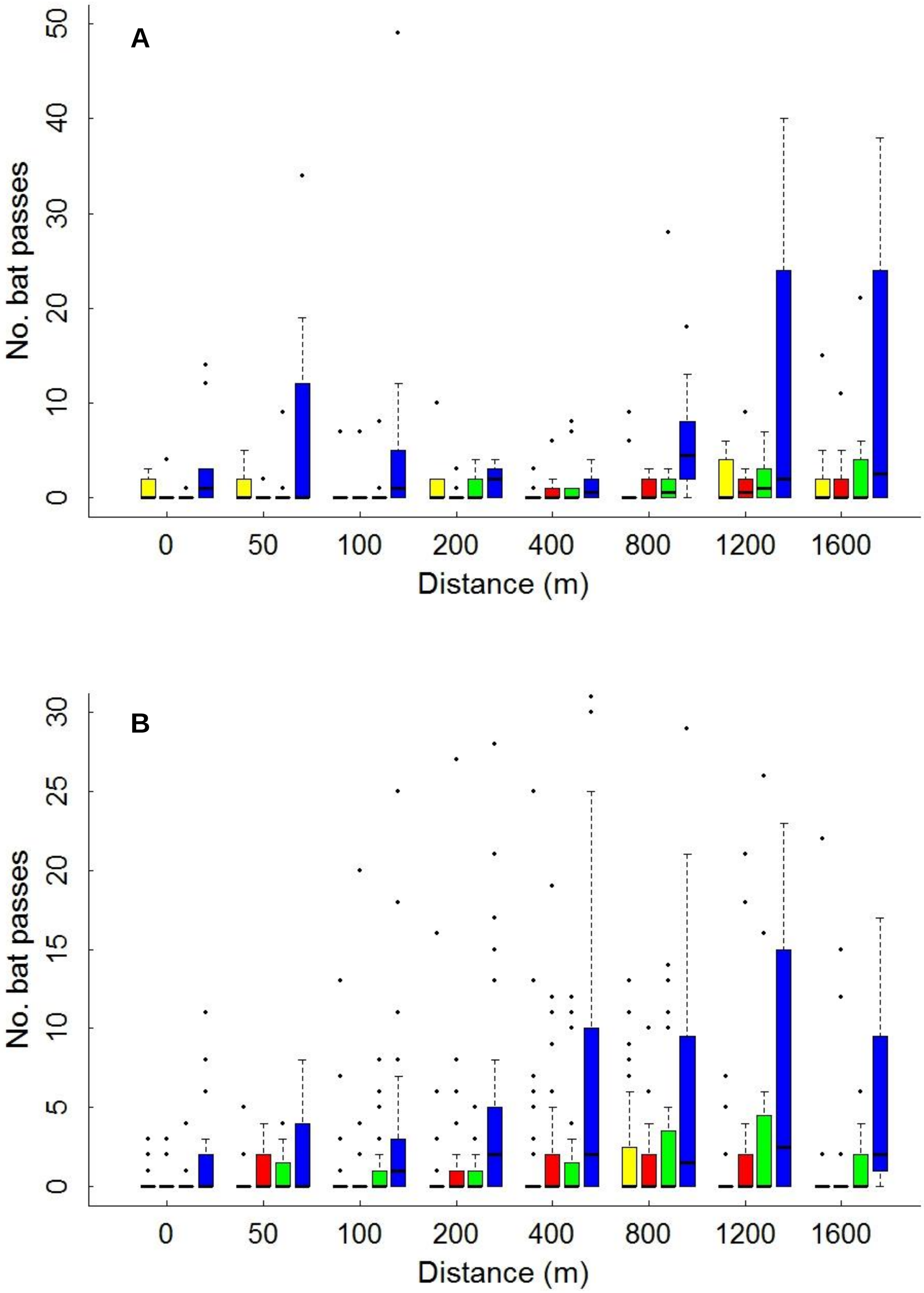

Figure 2.6: Boxplots of bat passes for each species/genus at each distance from the road.

Shows median with lower and upper quartiles and outliers, for 2009 data (A) and 2010 data (B) (Blue = *P. pipistrellus*, green = *P. pygmaeus*, red = *Myotis* spp., yellow = *Nyctalus* spp.). 2010 data have been cropped for clarity; see Figure 2.4 for full range of data points.

2.4.3 Effect on the number of species

The final ordinal logistic regression model was found to be significantly better than the null model (χ^2 = 24.9, d.f. = 2, P < 0.0001), and model assumptions of parallelism were met (χ^2 = 8.88, d.f. = 6, P > 0.05). The results showed that the number of species/genera increased with distance from the road (χ^2 = 5.59, d.f. = 1, P < 0.05) and habitat type (χ^2 = 21.42, d.f. = 1, P < 0.0001). The log odds of observing a greater number of species at 1,600 m from the road were found to be 2.5 times higher than at 0 m, and the log odds of observing a greater number of species in habitat types of grade 5 were found to be 6.2 times higher than in those of grade 1. The model also predicts a differential effect of distance from the road on the probability of observing a greater number of species/genera for each habitat type (Figure 2.7). Lower habitat grades show a greater increase in probability for more species/genera with distance from the road.

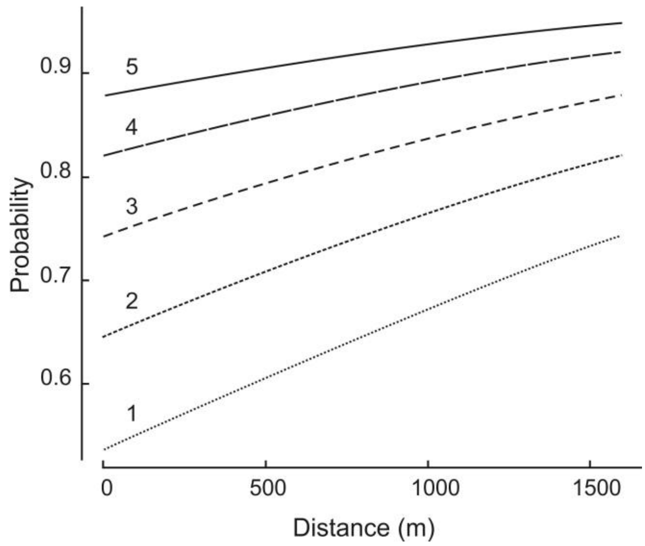

Figure 2.7: The probability of observing an increase of one bat species/genus with distance from the road in different habitat types.

Based on the predictions from the ordinal logistic regression model (habitat grades labelled as graded, 1 = low quality, 5 = high quality).

2.4.4 Noise effects

Traffic noise levels were not included in the GEE models as they were considered to be irrelevant to the scale of this study due to the short operating ranges observed. Noise levels decreased significantly with distance from the road (Kruskal-Wallis, χ^2 =

93.96, df = 44, $P < 0.0001$), but 89% of the change occurred in the first 50 m and no significant variation was found beyond 200 m (Figure 2.8).

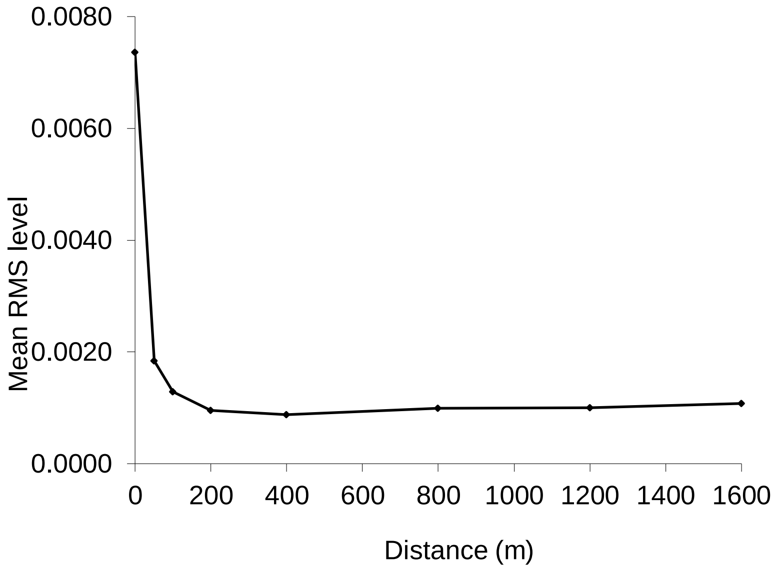

Figure 2.8: Traffic noise with distance from the road.

2.5 Discussion

2.5.1 The effects of time and habitat

Despite the short duration of the transects, time after sunset was found to have a significant effect on bat activity. This may reflect greater mobility following emergence before bats settle to forage at their regular sites. The activity of insectivorous bats is often bi-modal with a peak occurring a short time after sunset when initial commuting and foraging occurs, followed by reduced activity when bats may go to night roosts, with a second peak before sunrise prior to returning to the day roost (Hayes 1997). Potential bias was accounted for by performing transects in opposite directions and the effect of proximity to the road was consistent at all times.

Our aim was to minimise habitat heterogeneity to minimise bias caused by habitat preference. However, although large areas of woodland and water bodies were avoided, some variation in habitat was inevitable, as reflected in the habitat grading system used. As expected, bat activity and diversity increased with the increase in the height and continuity of tree and hedgerow cover along transects. This is supported by many other studies (Walsh & Harris 1996b; Walsh & Harris 1996a; Russ & Montgomery 2003; Frey-Ehrenbold *et al.* 2013). Also, the probability of observing more species groups away from the road increased most dramatically with distance for low habitat grades, suggesting that there are some subtle interactions between road effect, habitat and species that are worth further investigation.

2.5.2 Road effects

Despite a significant dependence on time and habitat type, we detected a marked independent decrease in bat activity and diversity in proximity to the road. This decline, to a distance of at least 1.6 km either side of the road, which for activity was consistent over 2 years, shows that major roads have a very significant impact on bat activity.

Possible reasons for lower activity and diversity closer to the road include habitat degradation due to light, noise and chemical pollution, a barrier effect, or increased mortality due to road kill. Although habitat quality will affect bat activity; habitat type as we assessed it (in terms of the height and continuity of tree and hedge cover) is not responsible for the lower bat activity found close to the road in this study. Noise pollution also cannot explain the result, since noise levels were low and unchanging beyond 200 m. Studies on the gleaning greater mouse-eared bat, *Myotis myotis,* (Schaub *et al.* 2008; Siemers & Schaub 2010) show that even species that hunt by listening for prey-generated noise are not likely to be affected by roads more than 60 m away. Light pollution was not addressed in this study, as the road sections studied were unlit. However, any effect of light pollution from road and vehicle lights is also likely to operate over short distances, due to the inverse square relationship between distance and light intensity. Road developments can disrupt local hydrology and polluted run-off may degrade wetland foraging habitats (Hellawell 1988; Highways Agency 2001). Automobile exhaust gases close to a road have been shown to be associated with a decline in arthropod diversity and abundance (Przybylski 1979). However, this effect is also unlikely to be important over long distances: the effects on invertebrates of lead and other metals from cars are limited primarily to 30 m from road sides (Motto *et al.* 1970; Muskett & Jones 1980). The many processes that may be degrading roadside habitats need further study, but none of those discussed are likely to explain changes in bat activity over 1.6 km.

However, reduced activity over large distances can be explained by the combination of a barrier effect and increased mortality due to roadkill. The home ranges of temperate insectivorous bat species typically extend 0.5 - 5 km from their roost (e.g. Bontadina *et al.* 2002; Senior *et al.* 2005; Davidson-Watts *et al.* 2006; Smith & Racey 2008), with most species showing high fidelity to roosts, foraging sites and commuting routes between them (e.g. Racey & Swift 1985; Entwistle *et al.* 2000; Senior *et al.* 2005). A major road built close to a nursery roost, and acting as a barrier to bats, will cause the colony home range to be reduced through both destruction of habitat and severance of commuting routes. Bats will be forced to forage in smaller areas or commute greater distances, either away from the road to find new foraging sites, or to find ‘safe’ crossing points along the road to commute to their original foraging sites. Mortality from roadkill is likely to be high since most species cross at heights that put them in the paths of vehicles (Verboom & Spoelstra

1999; Altringham 2008; Gaisler *et al.* 2009; Russell *et al.* 2009). These effects will reduce the reproductive output of nursery colonies (e.g. Tuttle 1976; Kerth & Melber 2009), and may force colonies to relocate, both leading to a fall in bat density near to the road, as observed in this study. In long-lived animals like bats, both reduced reproductive success and increased mortality will have a profound effect on local colony size and overall population size (Sendor & Simon 2003; Papadatou *et al.* 2011).

There is considerable evidence to suggest that roads act as barriers. Throughout our study only three bats were observed flying over the road, all *Nyctalus* species at heights above 20 m. *Nyctalus* species are known to fly high and to forage in open spaces (Kronwitter 1988), which is likely to make them less susceptible to the barrier effects of roads and collision mortality. The absence of other species of bat flying over the road suggests that the severance of linear elements by the road may have caused the abandonment of previous flight lines. Indiana bats, *Myotis sodalist,* reverse their flight paths and exhibit anti-predator avoidance behaviour in response to approaching vehicles (Zurcher *et al.* 2010; Bennett & Zurcher 2013). A recent study in Germany provides evidence for a strong barrier effect of a busy 4-5 lane road on Bechstein's bat, *Myotis bechsteinii*, a gleaning species (Kerth & Melber 2009). Female Bechstein's bats foraging close to the road had smaller foraging areas and lower reproductive success. Given the scale of the effects on bat activity in this study, it is highly likely that barrier and edge effects are negatively affecting the demographics and distribution of local bat populations in proximity to major roads. Similar effects have been found in other vertebrates. Reijnen & Foppen (1994) showed that a decreased density of willow warblers, *Phylloscopus trochilus,* up to 200 m from a major highway was due to the negative influence of the road on population sizes, with reduced breeding success and increased emigration of territorial males. Studies on breeding grassland birds revealed a decrease in density of seven out of 12 species, with disturbance distances up to 3,530 m from the busiest roads (50,000 vehicles per day), with collision mortality being a major contributor (Reijnen *et al.* 1996). A meta-analysis of 49 studies that between them investigated 234 bird and mammal species, found that bird population densities declined up to 1 km, and mammal population densities declined up to 5 km from roads (Benítez-López *et al.* 2010).

2.5.3 Species effects

The number of species recorded was found to decline in proximity to the road, which suggests that some species may be more affected by roads than others. Kerth & Melber (2009) found stronger effects of a major road on habitat use for the gleaning bat species *Myotis bechsteinii* than for *Barbastella barbastellus*, which forages in more open spaces. It is therefore possible that the foraging ecology of gleaning and woodland species in this study (e.g. *Myotis*) makes them more susceptible, whereas high fliers that are known to feed in open spaces (e.g. *Nyctalus*) may be less affected. A correlation between the strength of a barrier effect of a road and the foraging ecology of rainforest birds has also been found (Laurance *et al.* 2004). Although species-specific analyses were not possible, the significant positive effect of distance from the road observed for *Pipistrellus pipistrellus* was accentuated by the addition of the other species groups to the analysis. Given that *P. pipistrellus* is a generalist species (Vaughan *et al.* 1997; Nicholls & Racey 2006), likely to be more adaptable to habitat change and degradation, these effects are likely to be even greater for specialists such as *Myotis* and *Plecotus* species, explaining the increased species richness away from the road.

2.5.4 Conclusions and recommendations

This study reveals low bat activity and diversity either side of a well-established major road, showing that roads have a long term negative impact on bat populations. At least 80 km^2 of the landscape is affected for every 25 km of road. The scale of this impact indicates a barrier effect. Mitigation can remove the barrier and/or remove its impact. To remove the barrier we must make roads permeable and safe. Crossing points must connect effectively with known commuting routes to reduce the risk of abandonment and take bats safely under or over roads. Appropriate structures will be site specific and determined by local geography. Crossing structures have been installed throughout Europe in recent years, but due to inadequate and unfocused monitoring there are no data to assess their effectiveness at either individual or population level. We must assess the effectiveness of current structures and build only those shown to work. We should also further investigate the interaction between habitat and road effects, as our results suggest that improving habitat for bats around roads may compensate for some of the adverse impacts and reduce the barrier effect. Demographic effects will be slow to reveal themselves, and long term monitoring (> 10 years) may be necessary to provide an insight into the full effects of road developments and mitigation on bat populations.

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Chapter 3: The effect of a major road on bat activity and diversity in a landscape of high quality bat habitat

3.1 Abstract

We have provided evidence that roads can have a negative long term impact on bat activity and diversity, with the scale of the impact indicating a barrier effect. We also found evidence that habitat adjacent to the road interacts with the road effect, and improvements to the quality of this habitat can reduce the negative impact of roads on local bat populations. To further add to the evidence base, test the effect of other road developments in the UK, and explore the interaction between habitat and road effects, we repeated our transect study on a second road, the M5, in the south west of England. The M5 motorway is of a similar size, age and design to the M6 motorway used in the previous study, but is located in a region that is highly favourable to bats with a richer array of habitats and a better climate. As in the previous study, broadband acoustic surveys were conducted on 20 walked transects perpendicular to the road. Bat activity and habitat variables were recorded at eleven spot checks per transect at different distances from the road and the relationship between bat activity and these variables were investigated using generalised estimated equations (GEE), and ordinal logistic regression. Total bat activity and the activity of *Pipistrellus pipistrellus* (the most abundant species) were positively correlated with distance from the road, but the effect sizes were smaller than those found for the M6 motorway (by more than five times for total activity and three times for *P. pipistrellus* activity). Distance from the road was not found to have a significant effect on the number of bat species in this study. Although unseasonal weather was experienced during the study, the results suggest that the consistently high habitat grades found along transects by the M5 motorway may have reduced the negative impact of the road. Habitat improvements or compensatory habitat adjacent to roads may therefore be a useful mitigation measure for bats and should be explored further.

3.2 Introduction

Our study in Chapter 2 was one of the first to show that roads can have a major negative impact on bat foraging activity and diversity. Total bat activity, the number of bat species and the activity of the most abundant species, *Pipistrellus pipistrellus,* were all positively correlated with distance from the road. According to model predictions, between 0 and 1,600 m from the road total bat activity increased more than three-fold, *P. pipistrellus* activity increased more than two-fold, and the probability of observing a greater number of bat species increased by more than two and a half times. The scale of the impact over large distances indicates a barrier effect and increased mortality due to collisions with vehicles, both of which will reduce the home range size of local bat colonies and the reproductive output of nearby nursery colonies (e.g. Tuttle 1976; Kerth & Melber 2009), with serious consequences for the viability of local bat colonies and the overall population (Sendor & Simon 2003; Papadatou *et al.* 2011).

The study in Chapter 2 also showed that bat activity and diversity were positively affected by the height and continuity of nearby linear features. Bat activity was almost four times higher, and the probability of observing a greater number of species was more than six times higher in proximity to tall, continuous tree lines or hedgerows than in open landscapes. The use of linear features by bats for both foraging and commuting is supported by other studies (Walsh & Harris 1996b; Walsh & Harris 1996a; Russ & Montgomery 2003; Frey-Ehrenbold *et al.* 2013). This habitat effect also interacted with the negative impact of the road on bat diversity. The probability of observing more species with distance from the road increased more dramatically for low habitat grades (open landscapes) than high habitat grades (with tall continuous tree cover) (See Chapter 2, Figure 2.7). This suggests that the negative impact of roads on bat diversity may be reduced in higher quality habitats with well-connected linear elements. Increasing habitat quality around roads may therefore be a way to compensate for some of the adverse effects of roads. Improving remaining habitat or replacing lost habitat, as well as increasing connectivity between habitat patches may allow bat colonies to maintain home ranges equivalent to those prior to road construction.

3.2.1 The background of compensation mitigation

Major developments such as roads destroy, degrade and fragment habitats. Either replacing lost habitat or improving the quality of remaining habitat can be a way of compensating for these adverse impacts. The aim of such compensation is that there will be no net loss of habitat conditions or types, or to species populations, and it can be defined as 'the substitution of ecological functions or qualities that are impaired by development' (Cuperus *et al.* 1999). This compensation principle has been discussed in the literature with a variety of different terms being used such as 'ecological compensation', 'compensation mitigation', 'compensatory habitat', 'habitat banking' and 'mitigation banking' (e.g. Cuperus *et al.* 1999; Cuperus *et al.* 2001; Bedward *et al.* 2009; Briggs *et al.* 2009; Moilanen *et al.* 2009; Tischew *et al.* 2010). Compensation principles and subsequent legislation have been adopted in several countries, for example, the German compensation system (since 1976; cf. Meier 1987), the no-net-loss policy for wetlands in the US (since 1986; Section 404 of the Clean Water Act, cf. National Research Council 2001), the Dutch compensation principle for protected areas (since 1993; cf. MANF and MHPE 1993), the Swedish environmental compensation system (Swedish Parliament 1998), and the requirement in the UK for the obligatory compensation of losses to habitats or species in sites protected by the Natura 2000 network (Council of the European Community 1992). Compensation can take a variety of forms. It may involve the direct replacement or improvement of habitats in the vicinity of the development, or it may involve financial contributions to a 'bank' which will be put towards nature and landscape conservation in other areas, sometimes distant or unrelated to the development in question (Darbi *et al.* 2009). However, there is little evidence available to support the effectiveness of compensation measures such as habitat improvements in reducing the negative impact of developments. This is largely due to issues of non-compliance, poor goal setting and implementation, or insufficient monitoring (e.g. Quigley & Harper 2006; Gibbons & Lindenmayer 2007).

3.2.2 Aims of the study

The purpose of this study was to repeat the study in Chapter 2 on a second road development to: (1) verify whether the negative effects we found are also found at other sites, (2) further add to the evidence base for the effect of roads on bats, and

(3) test the hypothesis that increased habitat quality reduces the negative impact of roads on bats. The M5, a motorway of similar size, age and design to the M6 motorway in Chapter 2, was selected in the south west of England, a region that is highly favourable to bats with high quality bat habitat. The methods in Chapter 2 were repeated with some minor alterations and the results from both studies were compared.

3.2.3 Bat activity in the south west of England

We conducted our study along the M5 motorway in the south west of England across Somerset and part of North Devon. This region has a warmer, wetter climate than other parts of the UK, due to the warm temperature of the sea which surrounds the land on three sides. Precipitation occurs all year round, and the annual average minimum and maximum temperatures are 6 – 14 °C (Met Office 2013b) in inland areas of Somerset compared to the UK averages of 5 – 12 °C (Met Office 2013a). The region consists of rolling hills and large flat expanses of land, with a range of habitats including rich natural grasslands and wetlands, ancient woodlands and heathland. The predominant land use is agricultural grazing. The region has three Areas of Outstanding Natural Beauty (AONB) and supports a high proportion of some of the UK's rarest and most endangered habitats such as calcareous grassland and flower rich pastures (Biodiversity South West 2013). Somerset has 127 Sites of Special Scientific Interest (SSSI) and 5 Special Areas of Conservation (SAC) that are of international importance for bats (Natural England 2013b). This includes Beer Quarry and Caves in the Blackdowns Natural Area where more than 40% of the known UK population of *Myotis bechsteinii* bats hibernate, as well as nationally rare *Rhinolophus ferrumequinum* (Joint Nature Conservation Commitee 2013a; Natural England 2013a). Banwell Caves in the Mendip Hills AONB also provide important hibernation sites for *R. ferrumequinum* and *R. hipposideros* (Joint Nature Conservation Commitee 2013b).

The south west of England has been found to support at least 16 of the 17 bat species resident in the UK (*Myotis alcathoe* has only recently been discovered and its full distribution is not yet known). Most species are frequently recorded and all have been confirmed breeding in Somerset except for *Nyctalus leisleri* and

Pipistrellus nathusii (Somerset County Council 2013). Four species (*M. bechsteinii*, *Eptesicus serotinus, R ferrumequinum* and *R. hipposideros*) are found in isolation in the south west of the UK only.

3.3 Methods

3.3.1 Survey design

The survey design and methods used in Chapter 2 were repeated in this study, with some minor alterations, as detailed below. Acoustic surveys were conducted on walked transects approximately perpendicular to the M5, a major road in the south west of England, UK (Figure 3.1) between June and July 2012. Twenty transects were completed, each walked twice (Figure 3.2).

Figure 3.1: Photograph of the M5 motorway, Somerset, UK.

Taken near Taunton, looking north.

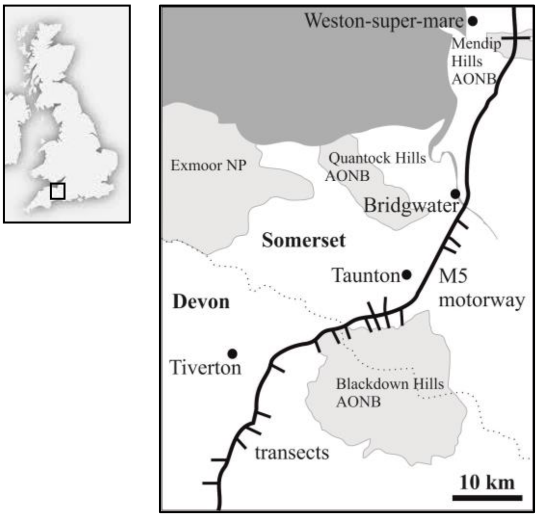

Figure 3.2: Map of the M5 study area and transect routes.

Black markers = transect routes, dark grey = Bristol Channel, light grey = protected areas: NP (National Park) / AONB (Area of Outstanding Natural Beauty).

The section studied consists of an 80 km stretch of road from Exeter in Devon to Weston-super-Mare in Somerset. The M5 (which runs from the middle of England to Exeter in the south west) is a well-established road, completed in 1977. It is a six-lane highway with a central reservation and a total width of 35 m or more. The maximum speed limit is 110 km h^{-1} and the traffic volume on the section studied is 25 - 90,000 vehicles per day (Average Annual Daily Traffic, Department for Transport 2011). This section of the M5 is predominantly unlit with the exception of interchanges, junctions and urbanised areas, and all transects were conducted along unlit sections.

Bat activity was recorded for 10 min at each of eleven spot checks along each transect at 0, 50, 100, 200, 400, 600, 800, 1000, 1,200, 1,400 and 1,600 m perpendicular to the road (e.g. Figure 3.3). This sampling regime was designed to detect even an effect restricted to the immediate vicinity of the road. Transects were selected using Ordnance Survey maps and site visits to assess their suitability. They were located either side of the road along minor roads or footpaths, through relatively homogenous habitat (avoiding large areas of woodland, water and human habitation) consisting of rural, undulating lowland dominated by grassland and agricultural pasture. Much of the study area contains a rich biodiversity of national and international importance.

Figure 3.3: Aerial photograph of a transect route.

Spot checks are shown as circles. © 2013 Google Earth © 2013 Getmapping plc.

Spot check locations were measured and marked using online mapping tools (EDINA, www.edina.ac.uk.) and (in the absence of suitable landmarks) a handheld GPS device (Garmin GPS 60Cx, www.garmin.com) to an accuracy of ± 10 m or better. Bat echolocation calls were automatically (high gain) detected using a Pettersson D240x broadband bat detector (www.batsound.com), with 100 ms time expanded (to 1 s) calls recorded directly to a solid state recorder (Edirol R-09HR, www.edirol.com) in mp3 (320 kbps) format to reduce file size for storage. One to three calls were captured in each 100 ms recorded segment, sufficient for identification. Each transect commenced 30 minutes after sunset to allow for varying emergence times of different species and was completed two and a half hours after sunset. To account for variation in activity patterns with time, all transects were walked in each direction (away from and towards the road) on separate nights. Transects were only completed in favourable weather conditions, avoiding wet, windy (> 20 km/h) or cold (< 7°C) nights.

Temperature and wind speed were also recorded at each spot check using a digital anemometer/thermometer (Techno line EA-3010, www.technoline.eu). Although transect routes were selected for their habitat homogeneity, the rich mosaic of habitats in the area meant that variation was still present. Habitat types were therefore recorded and classified into 5 categories as in Chapter 2 (Table 3.1). Traffic noise was not recorded as it is unlikely to have an effect beyond 200 m from the road (see Chapter 2, Figure 2.8).

Table 3.1: The criteria used to classify spot check habitat types

Grade	Habitat type
1	Fence or wall lining road/path & open fields beyond
2	Hedges/shrubby verges lining road/path & open fields beyond
3	Intermittent medium trees/bushes lining road/path & open fields beyond
4	Intermittent tall trees lining road/path & open fields beyond
5	Continuous tall tree cover lining road/path with woodland &/or open fields beyond

3.3.2 Acoustic analysis

Analysis of echolocation calls was carried out using Batsound Pro software (www.batsound.com). The mp3 files were converted to WAV format using Goldwave. Bat species were identified from the sonograms of their calls using call shape, end frequency and the maximum energy frequency or 'F_{maxe}' (Parsons & Jones 2000). In most cases, bats of the genera *Myotis* could not be identified to the species level due to similarity in call structure (Parsons & Jones 2000), and were therefore recorded to the genus level only. *Myotis nattereri* and *M. mystacinus* are known to be widespread in the area. *M. bechsteinii* are rare, and *M. brandtii* are common in the north and west of Somerset but rare elsewhere (Somerset County Council 2013). *M. daubentonii* are also known to be widespread in the area, but are less likely to have been recorded on our transects since they are confined almost exclusively to water courses. *M. alcathoe* may also be present, but we know little about its distribution due to the relatively recent discovery of this species within the UK. It can also be difficult to distinguish between *Nyctalus noctula, N. leisleri* and *Eptesicus serotinus* due to overlap of call parameters so a proportion of calls from these larger bat species were grouped into one guild (*Nyctalus*/*Eptesicus*). *E. serotinus* is widespread in the study area, *Nyctalus noctula* is less common and *N. leisleri* is rare. A small number of *Pipistrellus* calls (15%) were classified only to genus level, due to the overlap of call parameters of *P. pipistrellus* and *P. pygmaeus*. *P. nathusii* is very rare, and although some overlap with the calls of other *Pipistrellus* species can occur, it is not likely to have been recorded. The calls of *Plecotus* species are similar but recordings were likely to be the more commonly found *P. auritus* than *P. austriacus* which is very rare. However *P. auritus* will be under-recorded due to its low intensity echolocation call (Parsons & Jones 2000) and too few recordings were made for meaningful analysis of this species. The other bat species present in the area (*Rhinolophus ferrumequinum, R. hipposideros,* and *Barbastella barbastellus*) have distinct call types and can be easily distinguished.

The number of ‘bat passes’ was used as a measure of bat activity. A single bat pass was defined as one or more clearly recognisable echolocation call from a single species, separated from the next pass by a gap of at least one second. Measuring bat activity provides a good surrogate for bat density in the study area due to the fidelity of bat colonies to roosting and foraging sites (e.g. Senior *et al.* 2005).

3.3.3 Statistical analysis

A multiple regression model was built to investigate the relationship between bat activity and distance from the road, and examine the effects of other variables (time, habitat and climate) that could influence bat activity and hence the relationship. This was performed by fitting appropriate generalised estimating equations (GEE) using the *geeglm* function from the library *geepack* (Halekoh *et al.* 2006) in the R program, version 2.13.0 (R Development Core Team 2006). This approach accounts for within cluster correlation which violates the independence assumption in conventional regression analyses and leads to type 1 errors. GEE's adjust regression coefficients and variance to account for spatially and temporally correlated data, common in ecological research. A first order autoregressive model AR(1) was used to account for auto-correlation between spot checks conducted along the same route and on the same night. Transect routes were assumed to be independent. The jackknife estimation principle was used to avoid bias due to a small number of clusters (<30). Numbers of bat passes were transformed to log(count+1) to account for the presence of zero counts and large variations in activity observed between transect routes that resulted in heterogeneity. A Gaussian distribution with an identity link gave the best fit to the data. Explanatory variables used in the model were distance from the road, time after sunset, and habitat type. All two-way interactions were not significant and were excluded in the model selection process. Climatic variables were excluded from the analysis as variation was found to be significantly greater between nights and across the season than within nights so were accounted for by modelling the nightly variation in the dependence structure. Backward selection and Wald χ^2 tests were used to assess the overall significance of variables and produce the minimum adequate model. Plots of residuals were examined to check for normality and assess the appropriateness of the fitted model. The low abundance of most individual species or genera in this study does not allow for species-specific analysis, except for that of *P. pipistrellus*, for which the above model was repeated.

For the number of bat species/genera groups, a proportional odds ordinal logistic regression was performed using the *lrm* function from the library *Design* in the R program (Harrell 2009). Groups of species/genera were treated as ordinal categorical variables defined as 1 (0 species/genera), 2 (1 species/genus), 3 (2 species/genera) and 4 (3 or more species/genera). A robust Huber-White “sandwich” covariance estimator (Huber 1967) was applied using the R function *robcov* to correct for auto-correlation due to clustered samples (Harrell 2006), with clusters defined as in the GEE above. Explanatory variables were input as above and Wald χ^2 tests used for model selection. Appropriate graphical methods and statistical tests (χ^2 Test of Parallel Lines) were used to ensure model assumptions were met (Harrell 2006).

3.4 Results

3.4.1 Overall effects

A total of 2,967 bat passes were recorded during the study. The only significant variable in the GEE minimum adequate model for the transformed number of all bat passes was distance from the road (Figure 3.4, Table 3.2), which was found to have a significant positive effect on the number of bat passes (χ^2 = 5.78, d.f. = 1, P < 0.05).

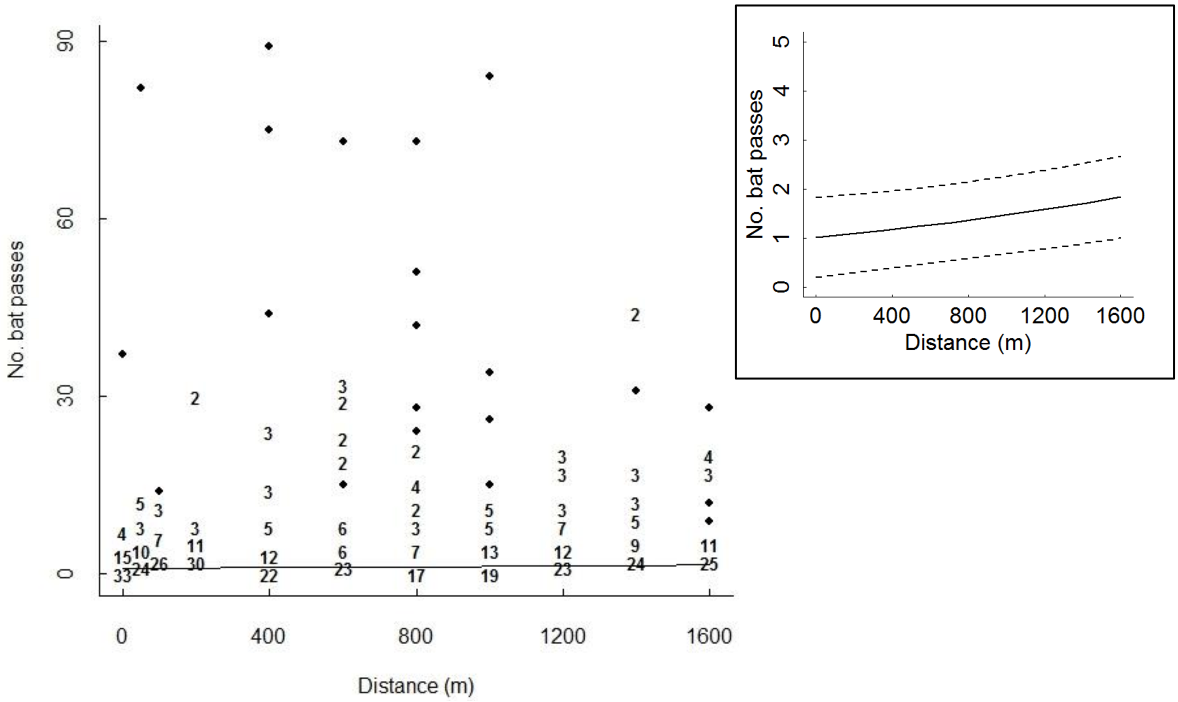

Figure 3.4: Effect of distance from the road on total bat activity as predicted by the minimum adequate GEE model.

Left: Model prediction with full range of data points (numbers represent replicate points), right: a close-up view of model predictions only. Dashed lines indicate approximate 95% confidence intervals.

Table 3.2: Results from the GEE analysis for total bat activity.

Modelling log (1 + number of bat passes) as a function of distance from the road (m).

	Bat passes (all species)	
Coefficients	Estimate	SE
Intercept	1.0052***	0.0883
Distance (m)	0.0003*	0.0001
Correlation parameter	0.345	0.0609
Scale parameter	1.3	0.0858

** P<0.05, *** P<0.001*

3.4.2 Species-specific effects

Ten species/genera were detected during the study. *Pipistrellus pipistrellus* was the most abundant species, making up 56% (n = 1646) of the total bat passes. The other species or species groups recorded were *Myotis* species (13%, n = 385), unidentified *Pipistrellus* species (11%, n = 335), *Eptesicus serotinus* (8%, n = 237), *Pipistrellus pygmaeus* (6%, n = 187), unidentified species of *Nyctalus*/*Eptesicus* guild (5%, n = 144), *Nyctalus noctula* (4%, n = 107), *Barbastella barbastellus* (<1%, n = 17), *Rhinolophus hipposideros* (<1%, n = 11), *Nyctalus leisleri* (<1%, n = 9), *Plecotus auritus* (<1%, n = 4) and *Rhinolophus ferrumequinum* (<1%, n = 1). The number of bat passes found at each distance from the road for each species or species group are shown in Figure 3.5.

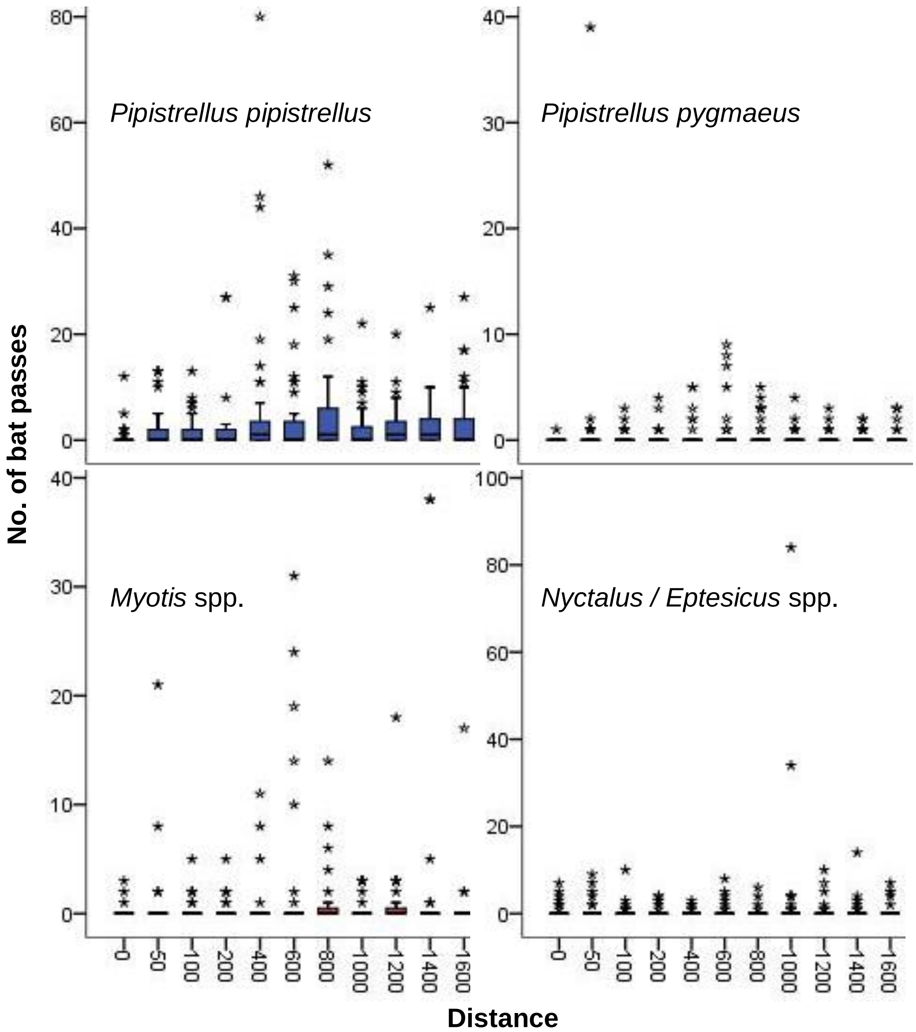

Figure 3.5: Boxplots of bat passes for each species/species group at each distance from the road.

Shows median with lower and upper quartiles and outliers. *Barbastella barbastellus*, *Plecotus auritus* and *Rhinolophus* spp., have been omitted due to low abundance.

The only species that was abundant enough for statistical analysis was *P. pipistrellus*. The results of the GEE minimum adequate model for the transformed number of *P. pipistrellus* passes reflect the results of the model for all bat passes (Figure 3.6, Table 3.3). The number of passes increased with distance from the road (χ^2 = 4.48, d.f. = 1, P < 0.05).

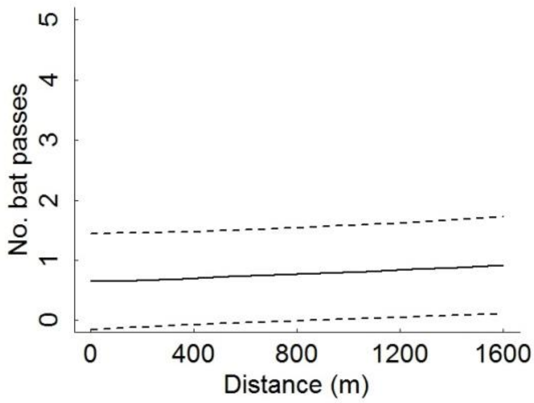

Figure 3.6: Effect of distance from the road on *Pipistrellus pipistrellus* activity as predicted by the minimum adequate GEE model.

Dashed lines indicate approximate 95% confidence intervals.

Table 3.3: Results from the GEE analysis for *Pipistrellus pipistrellus.*

Modelling log (1 + number *Pipistrellus pipistrellus*) as a function of distance from the road (m).

	P. pipistrellus passes	
Coefficients	Estimate	SE
Intercept	0.5615***	0.0782
Distance (m)	0.0002*	0.0001
Correlation parameter	0.31	0.0631
Scale parameter	1.01	0.0961

* *P<0.05, *** P<0.001*

3.4.3 Effect on the number of species

None of the variables entered into the ordinal logistic regression model were found to be significant predictors of the number of bat species/genera recorded (all P > 0.05). Time after sunset was the only variable which approached significance (P = 0.053), with the log odds of observing a greater number of species half an hour after sunset being 1.9 times higher than at two and a half hours after sunset.

3.4.4 Distribution of habitat types

Although habitat type varied with distance from the road there was not a simple relationship of increasing habitat 'quality' with distance (See Table 3.4), and habitat type was not a significant predictor of bat activity in the final GEE model. Most habitat grades are relatively evenly distributed across all distances showing that variation in habitat, as assessed, did not bias the results. The preferred habitat, grade 5, was actually found to be more frequent in proximity to the road, whereas the less favourable habitat, grade 2, was found to be more frequent at spot checks away from the road.

Table 3.4: The number of spot checks found to contain each habitat type.

As graded in this study, at each distance from the road.

Habitat grade	Distance (m)										
	0	50	100	200	400	600	800	1000	1200	1400	1600
1	2	2	6	0	0	0	0	0	2	0	0
2	6	6	4	6	6	0	6	6	6	10	8
3	6	6	6	12	4	2	4	4	3	6	4
4	6	6	12	8	12	18	16	13	17	18	18
5	20	20	12	14	18	10	14	17	12	6	10

For the purpose of comparison of road effects with the study in Chapter 2, habitat grades found adjacent to the M5 motorway were compared to those by the M6 motorway in Cumbria. The frequency of different habitat grades present along transects adjacent to the M5 was found to be significantly different to those by the M6 (χ^2 = 124.6, d.f. = 4, P < 0.0001). Habitat quality, as assessed, was higher around the M5 with a greater occurrence of higher habitat grades, whereas habitat around the M6 was dominated by lower habitat grades (Figure 3.7).

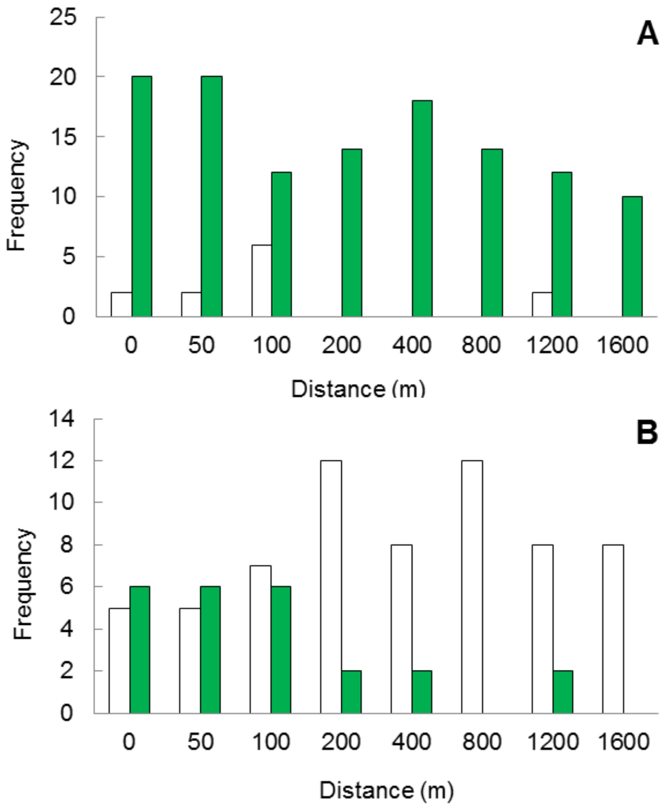

Figure 3.7: The total number of spot checks with habitat grades 1 and 5 at each distance from the M5 and M6 motorways.

A) M5 motorway, B) M6 motorway (white = habitat grade 1, green = habitat grade 5 in both).

3.4.5 Temperature

Significantly higher temperatures were recorded at spot checks along transects by the M5 than by the M6 (Figure 3.8; U = 16280, $P < 0.0001$).

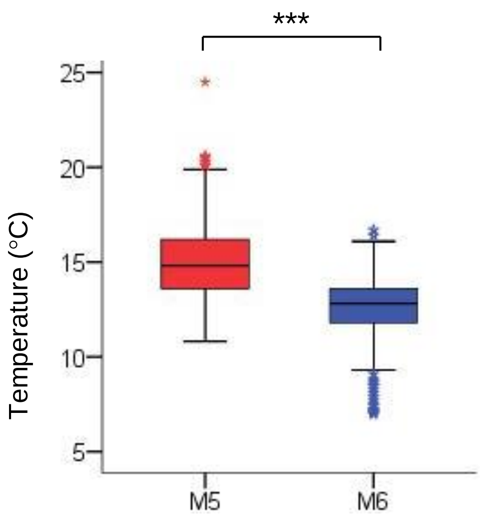

Figure 3.8: Boxplot of median temperature per spot check by the M5 and M6 motorways.

Shows upper and lower quartiles and outliers. *** $P < 0.0001$.

3.5 Discussion

3.5.1 Bat activity by the M5 motorway

Despite being in a region of the UK that is more favourable to bats with generally higher quality bat habitat, and the addition of three extra spot checks per transect, the total bat activity recorded in this study (2,967 bat passes) was less than that recorded in the 2010 study in Chapter 2 (3,407 bat passes). These results, contrary to the expected, are likely to be due to the exceptionally poor weather conditions experienced across the UK in the summer of 2012. Mean temperatures were the coolest since 1998 and were 0.7°C below average in June and 1°C below average in July (Met Office 2013c). June and July were also the wettest on record since 1776, with over 150% of normal levels of rainfall, with the south west of England being particularly affected (Met Office 2013c). Rain and low temperatures have been found to be negatively correlated with bat activity (e.g. Erickson & West 2002; Parsons *et al.* 2003). This will in part be due to a decreased availability of insect prey; many insects have species-specific temperature thresholds below which they don't fly (Taylor 1963). Rain also decreases the ability of bats to forage efficiently as their echolocation calls are attenuated more rapidly in humid conditions (Hartley 1989; Snell-Rood 2012), and their energetic demands are increased with wet fur (Voigt *et al.* 2011). In prolonged periods of adverse weather, the fitness of adult bats may be reduced and females may be unable to lactate resulting in the abandonment of young or starvation and a subsequent decrease in population sizes. In May 2012, The Bat Conservation Trust saw a 50% increase in calls to their helpline about grounded bats (Bat Conservation Trust 2012). Despite the unseasonal weather, the temperatures recorded along transects were still significantly higher in this study than in our previous study in the north west of England. Although we would have expected higher levels of activity in the south west of England, data were still sufficient for statistical analysis and the application of GEE models to test the effect of the road and other variables. However, these results must be treated with caution as unseasonal weather may affect bat activity patterns (e.g. Frick *et al.* 2012).

3.5.2 The effect of time and habitat

Time and habitat were not found to significantly affect bat activity in any of our models in this study. Although both variables were found to have a significant effect on bat activity in our previous study in Chapter 2, the methods were designed to account for these variables, and appear to have done so in this study.

3.5.3 Road effects

We detected a significant decrease in bat activity in proximity to the road, a result that supports the findings of our previous study in Chapter 2. By replicating our original study in an independent region of the UK we have provided further evidence that roads have a significant negative impact on bat activity. As found previously, there was a decline in bat activity to a distance of at least 1.6 km either side of the road providing further support for a large scale impact on bats. This effect is best explained by a combination of a barrier effect and collision mortality (as discussed in Chapter 2), as habitat degradation by light, noise and chemical pollution operate across smaller scales and are unlikely to have much of an effect beyond the immediate vicinity of the road (Muskett & Jones 1980; Schaub *et al.* 2008; Siemers & Schaub 2010).

Although we observed a negative impact of the road on bat activity in this study, the road effects were found to be considerably smaller than in our previous study. Our model predictions show that total bat activity increased by 50% between 0 and 1,600 m from the road, whereas in our previous study there was an increase of almost 300%. Similarly with the model predictions for *Pipistrellus pipistrellus*, activity increased by less than 50% between 0 and 1,600 m from the road compared to almost 150% in our previous study. Although species-specific analyses were not possible, the significant positive effect of distance from the road observed for *P. pipistrellus* was again accentuated by the addition of the other species groups to the analysis, suggesting negative impacts are likely for some of the other bat species recorded. Distance from the road was not found to have a significant impact on bat diversity in this study, as it did in our previous study.

The two roads studied both consist of six lanes with a central reservation, are of a similar design and a standard average width of 35 m. Both are of a comparable age, completed in the 1970s, allowing similar periods of time for local bat populations to adapt. The average minimum traffic volumes are similar (25,000 vehicles per day on the M5 and 30,000 on the M6) but the M5 has a greater range in the volume of traffic along its length and a higher maximum average of up to 90,000 vehicles per day compared to the maximum average of 40,000 vehicles per day on the M6. Given the higher traffic volumes on the M5, we might expect this to create a stronger barrier effect. For example, it has been found that bats veer away from commuting routes severed by roads more often as traffic noise levels increase (Bennett & Zurcher 2013). However, the road effect was reduced in proximity to the M5 in comparison to the M6.

These reduced road effects could be explained by the presence of consistently high habitat grades found along transects by the M5. In our previous study, the effect of habitat type, as assessed, was found to interact with the impact of the road on bat activity and diversity with a reduced effect in higher habitat grades. Also, the probability of observing more species with distance from the road increased more dramatically in open landscapes than in those with tall continuous tree or hedgerow cover. This suggests that the negative impact of roads on bat diversity is reduced in higher quality habitats with well-connected linear elements. In the M5 study area, continuous tall hedges and tree lines were common whereas open and less connected habitats were rare. This provides a contrast to the habitats recorded along transects by the M6 where open habitats were more common with absent or sparse linear elements (e.g. Figure 3.9). Not only were the habitats, as we assessed them, of better quality, but the landscape in the study area surrounding the M5 consists of a much richer array of habitats than those found around the M6 in Cumbria. Fifteen transects in this study passed through or were within 2 km of Sites of Special Scientific Interest (SSSI). Six of the transects were within 2 km of Special Areas of Conservation (SAC), and two transects passed through an SAC for bats.

Figure 3.9: Aerial snapshots of the typical landscape surrounding the M5 and M6 motorways.

A) The M5 near Angersleigh, Somerset, B) The M6 near Killington, Cumbria. © *2013 Google Earth © 2013 Getmapping plc.*

The results have strong implications for the use of habitat improvements around roads to compensate for adverse road effects. Replacing habitat lost during construction or that has been made inaccessible by the road, improving the quality of remaining habitat, and increasing habitat connectivity may allow local bat colonies to maintain home ranges equivalent to those prior to road construction. This would remove the need for bats to attempt to cross the road to reach original foraging habitat or to travel further to find new habitat. Habitat improvements that involve increasing the amount of tall vegetation cover in proximity to roads may also have the added benefit of masking noise and light pollution which carry further in open landscapes.

However, the practical difficulties of such mitigation must be considered. It relies on the availability of suitable land and the co-operation of landowners, although this situation may be eased by the integration of public interest or incentives into the design and implementation (Cuperus *et al.* 1999). Conflict may also arise if there is a loss of land for agriculture, which is already in decline in the UK due to developments (Department for Communities and Local Government 2011). For compensation measures to be effective they must be in place and fully functional prior to development, but this may be difficult due to the establishment time of some habitats, for example, the time lag for trees to grow and hedgerows to mature (Vesk *et al.* 2008). It may also be difficult to quantify the amount of compensation required to successfully mitigate adverse effects and the particularities of each site would need careful consideration (Gibbons & Lindenmayer 2007; Quétier & Lavorel 2011). It has been suggested that predictive modelling could be integrated into the planning process to predict the impacts of developments and subsequent compensation measures (Bedward *et al.* 2009). The cost of providing compensatory habitat must also be considered and this will depend on regional land prices and the site design and management required. The total cost for compensation measures for two Dutch road projects have been estimated to be 1.5% (US$5M) and 3.4% (US$14.5M) of the total road construction costs (US$330M and US$420M) (Cuperus *et al*. 1999). However, these were for extensive compensation areas for multiple species and habitats.

Cuperus *et al.* (1999) have put forward guidelines for habitat compensation as a method to counteract the general adverse impacts of roads on wildlife. Habitat lost directly to road construction may be compensated for by replacing with new habitat of equal size or quality, and degraded habitats may be restored, improved or enlarged to support the density of species present before development. Isolated habitat patches may also be connected to compensate for the fragmentation of habitat by roads. A combination of site-specific compensation measures associated with road construction are suggested to address the impacts of habitat loss, degradation and isolation. Compensation may be on-site (within the road effect zone) or off-site (outside the effect zone), but highly sensitive species may avoid inhabiting heavily impacted areas and benefit more from compensation outside of the effect zone. For such ecological compensation to be successful it is important to take into account the actual habitat conditions and qualities of the site prior to the development, and for compensation measures to be put in place prior to construction to allow time for new habitat to become established. Habitat availability and connectivity across the landscape must also be considered, and long term monitoring and performance reviews are essential to ensure that objectives are met.

3.5.4 Existing evidence for compensation mitigation

There is little evidence available to support the effectiveness of compensation measures such as habitat improvements in reducing the negative impacts of developments. A review of compensation measures used to counteract the environmental impacts of road construction found that 26 of 57 compensation areas had to be excluded from the analysis due to poor goal setting, unclear implementation or failure to carry out the measures (Tischew *et al.* 2010). Analysis of the remaining 31 compensation areas, including 119 compensation sites, found that two thirds of the compensation goals set were only partly met or not met at all, with unsuitable site conditions, improper implementation and deficient management and follow up being major contributors to failure (Tischew *et al.* 2010). Compensation measures have also been discussed for road developments in Sweden, but are rarely used or documented (Rundcrantz 2006). A review of 72 road and railway Records of Decision in Spain found that compensation measures are rarely considered in Environmental Impact Assessments (Villarroya & Puig 2013).

Most attempts at compensation measures have been to protect habitats rather than specific species. Although it has been suggested that the success of compensation for protected species may be more effective than attempting to recreate whole habitats that are equivalent to lost habitat in function and integrity (Briggs *et al.* 2009), the evidence in support of this is lacking. Quantifying the success of compensation measures for protected species may also be more straight-forward than for whole habitats, provided rigorous monitoring is carried out with appropriate pre-construction baseline data and sufficient long term post construction monitoring

(Morris *et al.* 2006; Briggs *et al.* 2009). However, this is rarely completed and little evidence is available to support the success of compensation measures for protected species. Petranka *et al.* (2003) created compensatory ponds for amphibians and found that they were colonized rapidly and supported significantly more species than natural reference ponds within one to two years, although the need for longer term monitoring is stressed. A review of 26 peer-reviewed articles found that amphibian abundance or species richness was similar or higher at constructed or restored wetlands than at reference wetlands or historic surveys in 89% of studies (Brown *et al.* 2012). Balcombe *et al*. (2005) found similar avian abundance and species richness and higher water bird, waterfowl and anuran abundance and richness at 11 wetland mitigation sites in the USA (constructed 3-10 years previously) than at reference sites.

There is no evidence of compensatory habitat as mitigation for bats, but there is evidence from restoration projects that bats do respond positively to habitat improvements. In restored wetland habitats in the US, bat activity was found to be higher over restored wetlands than reference wetlands one year after development (Menzel *et al.* 2005), and Smith and Gehrt (2010) found that bats responded positively overall to woodland restoration in urban landscapes. However, robust pre- and post-construction monitoring is essential to assess the full impact on bat populations and the effectiveness of such measures in maintaining local bat colonies.

3.5.5 Conclusions and recommendations

We detected a significant decrease in bat activity in proximity to a second major road development in the UK on a large scale, supporting our previous findings and adding to the evidence that roads do have a major negative impact on bats through a combination of a barrier effect and increased mortality due to roadkill. The road effect, however, was reduced in this study with a smaller effect on bat activity and a lack of a significant effect on bat diversity. Although overall bat activity was lower than expected in this region of the UK and unseasonal weather must be taken into consideration, this result could be explained by the consistently higher quality bat habitat of well connected, mature linear elements and richer habitat types around the road in this study. Given the similarities in size, age, and design of the roads we studied and the expected effects of traffic volumes, this explanation is plausible and warrants further investigation. Compensatory habitat around roads created by replacing lost habitat, improving remaining habitat and increasing connectivity between habitat patches may therefore be a useful mitigation strategy for negating the adverse impacts of road developments on bats. Although such techniques have been employed for other wildlife in the past, they are often neglected in the planning process and poor implementation and monitoring has resulted in little evidence with which to assess their effectiveness (e.g. Tischew *et al.* 2010; Villarroya & Puig 2013). Cuperus *et al.* (1999) proposed general guidelines for the use of compensation measures for wildlife affected by road developments, and suggested that such measures are used in conjunction with other mitigation features such as safe crossing structures over roads. However, it is imperative that the effectiveness of such structures is proven prior to implementation, and this has not yet been done. We suggest that compensatory habitat around roads should be tested as a mitigation strategy for bats. This must be done with careful planning, implementation and thorough monitoring both prior to construction and in the long term to fully reveal the effect on local bat populations.

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Chapter 4: A comparison of acoustic data collection methods to study the effect of roads on bats

4.1 Abstract

Bats are challenging to study as they are typically small, fast flying and nocturnal. Until advances in bat detector technology, it was almost impossible to collect data on many aspects of bat ecology and behaviour for quantitative study. Bat detectors are now widely used to record the high frequency echolocation calls of bats, providing a measure of bat activity and a tool to identify bat species from their unique vocalisations. Different types of bat detector are available, all with associated advantages and disadvantages. We used time expansion bat detectors to record bats at spot checks along walked transects perpendicular to roads in Chapters 2 and 3, to reveal the negative impact of roads on bat activity and diversity. During the study in Chapter 3, we simultaneously made recordings of bat activity using a recently developed method of acoustic data collection called direct sampling. We compared the data collected with time expansion and direct sampling methods, and for both datasets the relationship between bat activity and diversity and distance from the road was investigated using generalised estimated equations (GEE), and ordinal logistic regression. Significantly more data was collected with direct sampling methods than time expansion methods, with more bat passes recorded per spot check. For both sampling methods, total bat activity and the activity of *Pipistrellus pipistrellus* (the most abundant species) were positively correlated with distance from the road, but effect sizes were approximately three times greater for the dataset recorded by direct sampling. Distance from the road was not found to have a significant effect on the number of bat species for either dataset. The study of bats can be constrained by the methods of data collection and technology available, and care should be taken when interpreting bat detector studies. Direct sampling combined with automatic call identification provides a more rapid, more objective and more precise measure of bat activity and diversity than alternative approaches.

4.2 Introduction

4.2.1 Bats and echolocation

Bats have evolved a highly advanced form of echolocation which enables them to successfully detect and capture insect prey at night, as well as navigate and spatially orientate themselves (Schnitzler *et al.* 2003). Bats transmit short ultrasonic pulses from the larynx, which are emitted through the nostrils or mouth, and sensitive auditory systems analyse the returning echoes in order to build an 'echo-picture' of their surrounding environment (Surlykke *et al.* 2009). The evolution of echolocation has allowed bats to exploit a previously little used ecological niche through nocturnal predation, contributing to the success of this large and diverse order. The characteristics of bat echolocation calls differ between species (e.g. Figure 4.1), and are adapted to habitat use and foraging ecology (Simmons *et al.* 1979; Schnitzler & Kalko 2001).

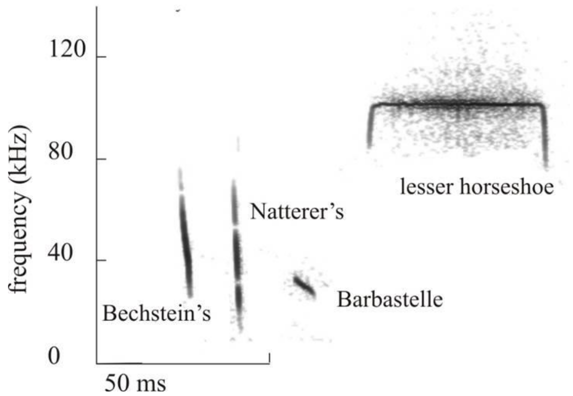

Figure 4.1: Sonograms of bat calls.

Time versus frequency plots of echolocation calls of *Myotis bechsteinii, Myotis nattereri, Barbastella barbastellus, Rhinolophus hipposideros.*

Bats that hunt in the open, such as *Nyctalus* species, typically use long, low frequency, narrowband calls to search for prey. These calls carry over a greater distance as the energy is concentrated into a narrow range of frequencies, and lower frequency calls are attenuated less rapidly in air (Hartley 1989). Bats that forage in and around cluttered vegetation, such as *Myotis* and *Plecotus* species, typically use higher frequency, broadband calls that sweep a range of frequencies, often with harmonics. These calls are attenuated more rapidly in air but provide a greater perception of detail and target discrimination at close range (Simmons 1971; Hartley

1989). Some bat species have a high degree of plasticity in their calls and can alter them according to habitat structure, for example *Pipistrellus* species significantly increase the bandwidth of their calls when foraging in cluttered environments (Kalko & Schnitzler 1993).

4.2.2 Acoustic analysis of bat calls

Bats are difficult to study as they are nocturnal, small, highly mobile, and often fast flying. At night, visual observation is difficult and identification of species in flight is usually impossible. Radio tracking may be useful for studying individuals but is labour intensive and can be used to address only a limited range of questions. The capture of bats, using mist nets or harp traps, is also laborious, highly skilled work that disrupts the natural behaviour of bats, and typically has a low success rate (e.g. Berry *et al.* 2004; Larsen *et al.* 2007). The development of bat detectors, tools with which to detect the echolocation calls of bats, has vastly improved our ability to study these mammals in a non-invasive way and collect large amounts of data with which to study their behaviour at the population level. Echolocation calls may be recorded and counted to quantify bat activity, a good surrogate for bat density due to the fidelity of bat colonies to roosts and foraging sites (e.g. Senior *et al.* 2005).

Spectrograms of bat echolocation calls can be examined using sound analysis software to identify calls to species or genus. Specific call characteristics can be measured such as pulse duration, the start and end frequency of calls, and the frequency within the call with the maximum energy or 'F_{maxe}' (Parsons & Jones 2000). These simple parameters allow for the manual identification of species with distinctive call types. However, overlap between calls of species within a genus, for example *Myotis* species, can occur making distinction difficult (Parsons & Jones 2000). Recently, automated methods for the identification of bat calls have been developed using machine learning algorithms such as random forests, support vector machines and artificial neural networks (e.g. Redgwell *et al.* 2009; Armitage & Ober 2010; Scott 2012; Walters *et al.* 2012). Models are trained on a library of reference echolocation calls, and programmed to use complex criteria for fast, often highly reliable classification of bat calls to the species level for all genera in the UK.

4.2.3 Bat detector technology

Until recently, the three most common methods for the acoustic detection of bats were heterodyne, frequency division and time expansion. There are advantages and disadvantages to all of these methods, but time expansion was the only technique where information was not lost from the incoming signal, making it the most suitable of the three methods for detailed acoustic analysis (Parsons *et al.* 2000). Time expansion operates by playing back detected echolocation calls, captured using high frequency microphones and rapid digital storage, at a slower speed. This decreases the frequency of the call to the human audible range and enables recordings to be made with conventional recorders for later analysis. A time expansion factor of ten is commonly used where playback speeds are decreased tenfold (e.g. 0.1 s replayed over 1 s). The disadvantage of time expansion is that continuous recording is not possible. Most modern detectors are only capable of storing and replaying a few seconds at a time and detection is not possible during playback, resulting in a major loss of sampling time (e.g. Figure 4.2).

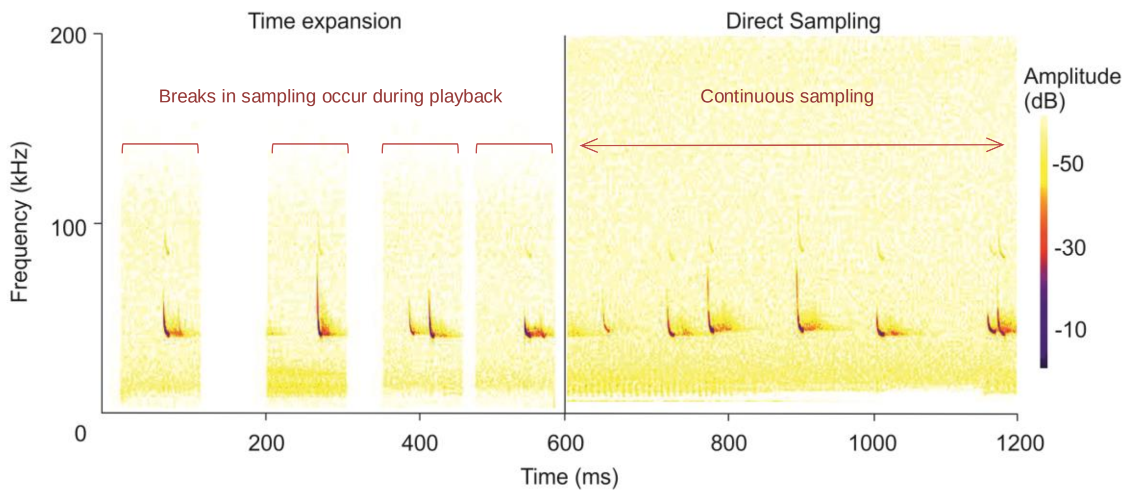

Figure 4.2: Spectrograms of *Pipistrellus pipistrellus* calls from recordings made with time expansion and direct sampling methods.

Recent advances in digital technology have resulted in a new method for recording bat echolocation calls; direct sampling. In this, full spectrum ultrasound is directly sampled and stored in real time allowing continuous recordings to be made, limited only by the amount of available storage space. These devices sample at very high rates (up to 500 kHz), capturing all signal information and allowing for detailed analysis of call structure. Large amounts of high quality data can be generated without a loss in sampling time, providing a more accurate picture of the bat activity being recorded than with time expansion methods (e.g. Figure 4.2). The recent development of automated acoustic analysis software particularly complements direct sampling methods, as it can quickly analyse the larger volumes of data produced that would be too time consuming to analyse manually.

4.2.4 Acoustic data collection methods for studying road effects

In Chapters 2 and 3 we used time expansion methods to detect and record bat echolocation calls to provide a measure of bat activity and diversity and investigate the impact of roads on bats. We used manual call classification methods to count the number of bat passes and identify calls to species or genus. In order to investigate the use of recently developed, more advanced methods for the detection and analysis of bat calls, we simultaneously recorded bat activity by direct sampling methods alongside time expansion devices in our study in Chapter 3. The direct sampling data were subsequently analysed using automated classification, and the differences in the negative road effects detected on bats by each method were compared.

4.3 Methods

We used the data collected in Chapter 3 with time expansion bat detectors, alongside data collected simultaneously with direct sampling detectors. The methods are given below in brief. For a more detailed description of the survey design, see Chapter 3.

4.3.1 Survey design

Acoustic surveys were conducted on 20 walked transects (each walked twice) approximately perpendicular to the M5, a major road in the south west of England, UK (Chapter 3, Figure 3.1 & 3.2) between June and July 2012. Transects were located either side of the road along minor roads or footpaths, through relatively homogenous habitat (avoiding large areas of woodland, water and human habitation) consisting of rural, undulating lowland dominated by grassland and agricultural pasture. Bat activity was recorded for 10 min at each of eleven spot checks along each transect at 0, 50, 100, 200, 400, 600, 800, 1000, 1,200, 1,400 and 1,600 m perpendicular to the road. The habitat at each spot check was graded according to the height and continuity of linear features such as hedgerows and treelines (Chapter 3, Table 3.1). Each transect commenced 30 minutes after sunset and was walked once in each direction (away from and towards the road) on separate nights. Transects were only completed in favourable weather conditions, avoiding wet, windy (> 20 km/h) or cold (< 7°C) nights.

4.3.2 Acoustic data collection methods

Bat echolocation calls were recorded using two different methods simultaneously at each spot check:

(1) Calls were automatically (high gain) detected using a Pettersson D240x broadband time expansion bat detector (www.batsound.com), with 100 ms capture periods expanded to 1 s, and recorded directly to a solid state recorder (Edirol R-09HR, www.edirol.com) in mp3 (320 kbps) format to reduce file size for storage. Recording commenced immediately after the 100 ms capture

period ended and the detector was re-armed after the 1 s download time. Thus, only 100 ms of sound was captured every 1100 ms.

(2) Calls were directly sampled using a Pettersson D500x ultrasound recording unit (www.batsound.com), set to trigger automatically on the detection of ultrasound and record for ten second periods with a sampling rate of 500 kHz. Recordings were stored internally as 16 bit WAV files onto removable compact flash cards. The trigger threshold and gain were kept constant throughout the study.

To ensure both devices were detecting bats within the same area, the sensitivity and detection range of the detectors were calibrated prior to the study. During data collection, the detectors were secured together with the microphones adjacent and pointing in the same direction.

4.3.3 Acoustic analysis methods

Time expanded calls were analysed manually using Batsound Pro software (www.batsound.com). The mp3 files were converted to WAV format using Goldwave (www.goldwave.com). Bat species were identified where possible from the sonograms of their calls using call shape, end frequency and the maximum energy frequency or 'F_{maxe}' (Parsons & Jones 2000). Due to the overlap of call parameters not all bats could be identified to the species level, and calls were categorised into nine species, genera or species groups, as described in Chapter 3 (*Barbastella barbastellus, Myotis* spp., *Nyctalus/Eptesicus* spp., *Pipistrellus pipistrellus, P. pygmaeus,* Unidentified *Pipistrellus* spp., *Plecotus auritus, Rhinolophus ferrumequinum* and *R. hipposideros*).

Direct sampling generated larger volumes of data, and for quick analysis, recorded calls were analysed using the automated call identification software, Bat Bioacoustics (Scott 2012). Calls classified to a confidence level of 90% or over were used for further analysis. Although the software can reliably classify nearly all UK bat species, calls were grouped according to the species or genera that can be identified manually (see above) to allow for direct comparison of detector methods.

For both methods, the number of ‘bat passes’ was used as a measure of bat activity. A single bat pass was defined as one or more clearly recognisable echolocation call from a single species, separated from the next pass by a gap of at least one second.

4.3.4 Statistical analysis of road effects

The relationship between bat activity, distance from the road, time and habitat types were investigated for both data collection methods by fitting generalised estimating equations (GEE) using the *geeglm* function from the library *geepack* (Halekoh *et al.* 2006) in the R program, version 2.13.0 (R Development Core Team 2006). This approach was used to account for within cluster correlation which violates the independence assumption in conventional regression analyses and leads to type 1 errors. GEE’s adjust regression coefficients and variance to account for spatially and temporally correlated data, common in ecological research. In this study, a first order autoregressive model AR(1) was used to account for auto-correlation between spot checks conducted along the same route and on the same night. Transect routes were assumed to be independent. The jackknife estimation principle was used to avoid bias due to a small number of clusters (<30). Numbers of bat passes were transformed to log (count+1) to account for the presence of zero counts and large variations in activity observed between transect routes that resulted in heterogeneity. A Gaussian distribution with an identity link was used which gave the best fit to the data. Explanatory variables used in the model were distance from the road, time after sunset, and habitat type. All two-way interactions were not significant and were excluded in the model selection process. Climatic variables were excluded from the analysis as variation was found to be significantly greater between nights and across the season than within nights so were accounted for by modelling the nightly variation in the dependence structure. Backward selection and Wald χ^2 tests were used to assess the overall significance of variables and produce the minimum adequate model. Plots of residuals were examined to check for normality and assess the appropriateness of the fitted model. The low abundance of most individual species or genera in this study did not allow for species-specific analysis, except for that of *P. pipistrellus*, for which the above model was repeated.

For the number of bat species/genera groups, a proportional odds ordinal logistic regression was performed using the *lrm* function from the library *Design* in the R program (Harrell 2009). Groups of species/genera were treated as ordinal categorical variables defined as 1 (0 species/genera), 2 (1 species/genus), 3 (2 or more species/genera). It was not possible to have more than three categories due to the infrequency of recording three or more species together at spot checks. A robust Huber-White “sandwich” covariance estimator (Huber 1967) was applied using the R function *robcov* to correct for auto-correlation due to clustered samples (Harrell 2006), with clusters defined as in the GEE above. Explanatory variables were input as above and Wald χ^2 tests used for model selection. Appropriate graphical methods and statistical tests (χ^2 Test of Parallel Lines) were used to ensure model assumptions were met (Harrell 2006).

4.4 Results

4.4.1 Overall effects

A total of 2,967 bat passes were recorded using the time expansion method, and 19,674 bat passes were recorded using the direct sampling method. The number of bat passes recorded per spot check was significantly higher using direct sampling than time expansion (Figure 4.3; Wilcoxon test, $Z = -11.7$, $P < 0.0001$). Bats were detected at a total of 288 spot checks using time expansion and 298 spot checks using direct sampling. At 15% of spot checks (n = 63) bats were detected by the time expansion detector only, and at 19% of spot checks (n = 80) bats were detected by the direct sampling method only. However, there was no significant difference between the number of spot checks where bats were detected using either method ($\chi^2 = 0.17$, d.f. = 1, $P > 0.05$).

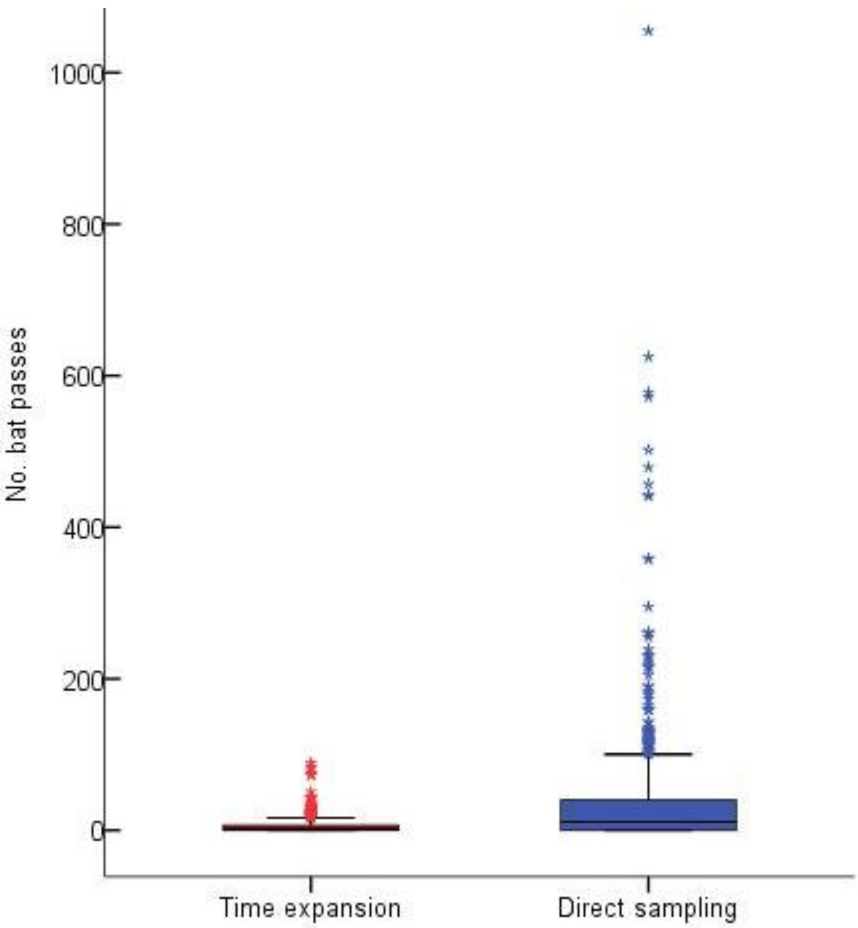

Figure 4.3: Boxplot of total bat passes recorded per spot check for each detection method.

Shows median (time expansion = 2, direct sampling = 11) with lower and upper quartiles and outliers.

The results of the GEE for the direct sampling data support those from the time expansion data, with distance from the road being the only significant variable in the minimum adequate model for the transformed number of all bat passes (χ^2 = 7.31, d.f. = 1, P < 0.01; Figure 4.4, Table 4.1). Model predictions for the effect of the road on total bat activity are larger for the direct sampling data with an increase in activity of 156% between 0 and 1,600 m from the road, compared to 52% for the time expansion data (Figure 4.4).

Table 4.1: Results from the GEE analysis for total bat activity for each detection method. Modelling log (1 + number of bat passes) as a function of distance from the road (m).

	Time expansion Bat passes (all species)		**Direct sampling** Bat passes (all species)	
Coefficients	Estimate	SE	Estimate	SE
Intercept	1.0052***	0.0883	1.8263***	0.1612
Distance (m)	0.0003*	0.0001	0.0006**	0.0002
Correlation parameter	0.345	0.0609	0.393	0.0643
Scale parameter	1.3	0.0858	3.53	0.163

** P < 0.05, ** P < 0.01, *** P < 0.001*

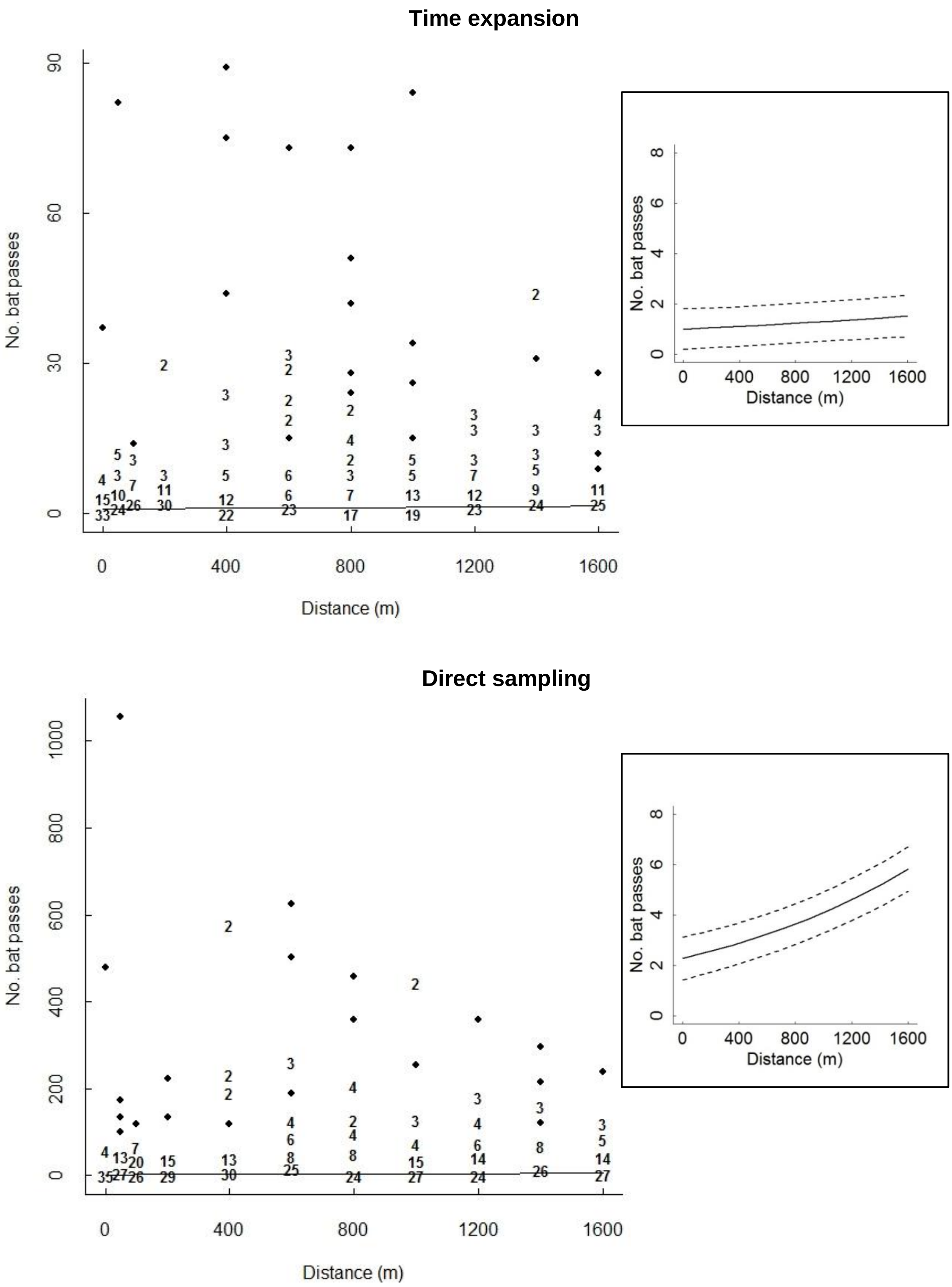

Figure 4.4: GEE predictions for both acoustic data collection methods.

Time expansion (top), direct sampling (bottom). Solid lines in all plots show the effect of distance from the road on the number of bat passes as predicted by the minimum adequate GEE. Left plots show the full range of data points (numbers represent replicate points), right plots show a close-up view of model predictions only. Dashed lines indicate approximate 95% confidence intervals.

4.4.2 Species-specific effects

Bats were detected for each of the nine species, genera or species groups used for classification. The direct sampling method recorded significantly more bat passes per spot check for all of the species or species groups recorded (all $P < 0.05$), but the proportions of species recorded were similar between methods (Figure 4.5).

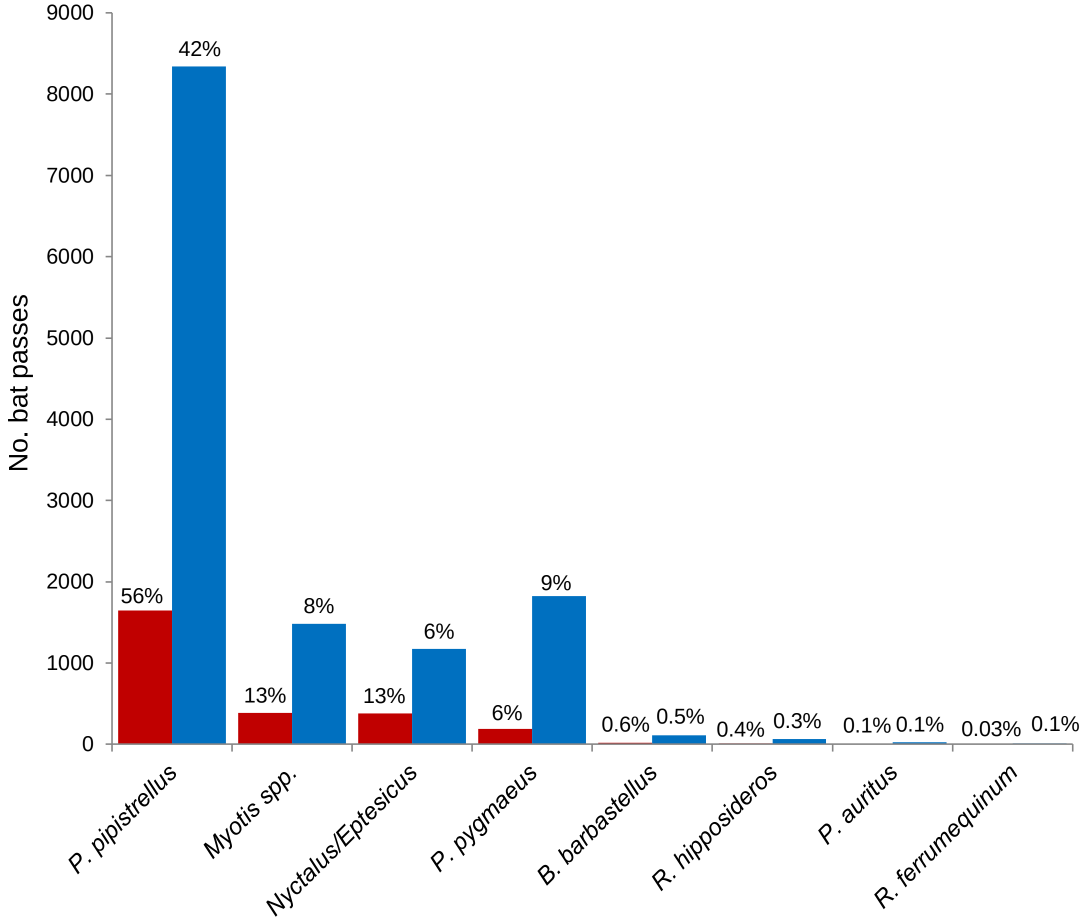

Figure 4.5: The total number of bat passes recorded by each detection method for each species or species group.

Red = Time expansion, blue = direct sampling. Percentages show the proportion of bat passes for each species group of the total recorded by each method.

Although the direct sampling method produced more data, the less abundant species were still absent from a large proportion of the spot checks providing insufficient information for modelling. The number of bat passes recorded by time expansion or direct sampling, at each distance from the road for each species or species group are shown in Figure 4.6.

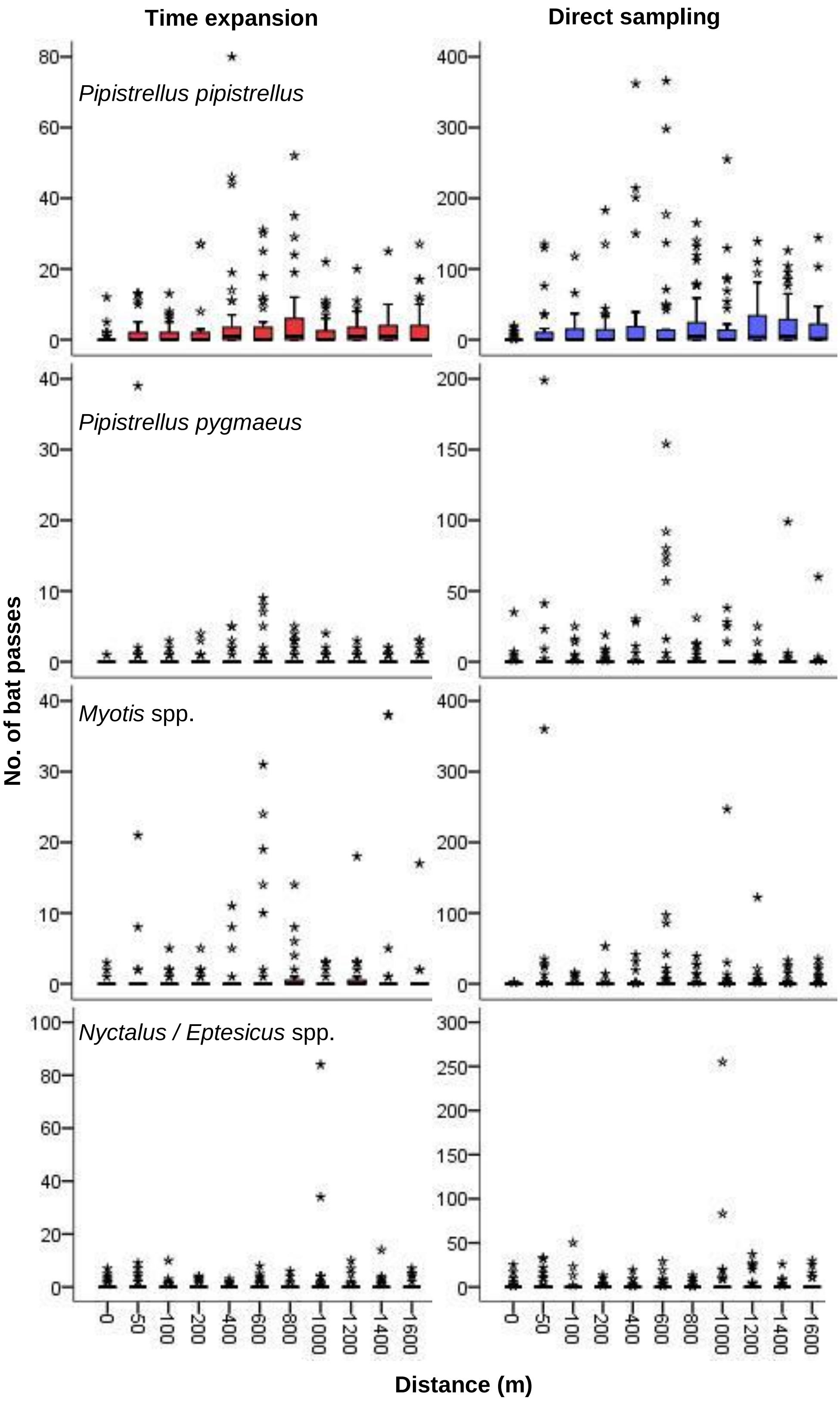

Figure 4.6: Boxplots of bat passes for each species or species group recorded by each detection method at each distance from the road.

Shows median with lower and upper quartiles and outliers. Note the change in y axes. *Rhinolophus* spp. and *Barbastella barbastellus* have been omitted due to low abundance.

The only species that was abundant enough for statistical analysis was *Pipistrellus pipistrellus*. The results of the GEE minimum adequate model for the transformed number of *P. pipistrellus* passes from the direct sampling method reflect the results of the model for the time expansion model (Figure 4.7, Table 4.2), with the number of passes increasing with distance from the road (χ^2 = 4.48, d.f. = 1, P < 0.05). Model predictions for the effect of the road on *P. pipistrellus* activity are again larger for the direct sampling data with an increase in activity of 119% between 0 and 1,600 m from the road, compared to 42% for the time expansion data.

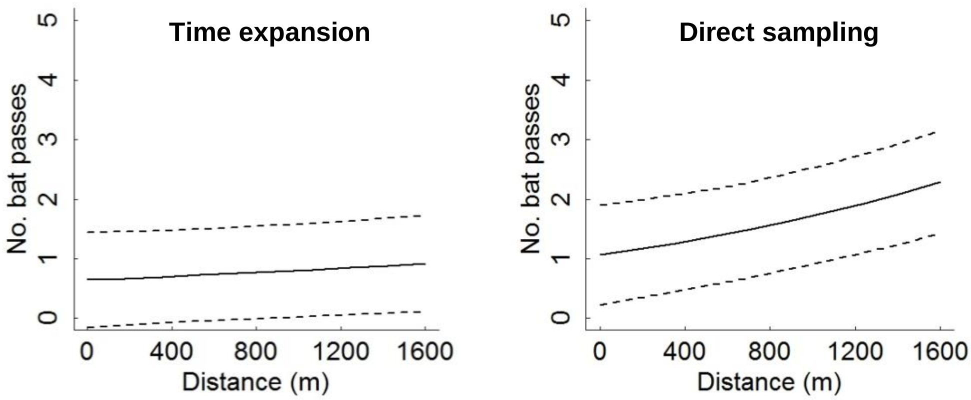

Figure 4.7: Effect of distance from the road on *Pipistrellus pipistrellus* activity as predicted by the minimum adequate GEE model for each detection method.

Dashed lines indicate approximate 95% confidence intervals.

Table 4.2: Results from the GEE analysis for *Pipistrellus pipistrellus* for each detection method.

Modelling log (1 + number *Pipistrellus pipistrellus*) as a function of distance from the road (m).

	Time expansion *P. pipistrellus* passes		**Direct sampling** *P. pipistrellus* passes	
Coefficients	Estimate	SE	Estimate	SE
Intercept	0.5615***	0.0782	1.0220***	0.1348
Distance (m)	0.0002*	0.0001	0.0005**	0.0002
Correlation parameter	0.31	0.0631	0.309	0.0763
Scale parameter	1.01	0.0961	2.9	0.193

** P<0.05, ** P<0.01, *** P<0.001*

4.4.3 Effect on the number of species

For the time expansion data, none of the variables entered into the ordinal logistic regression model were found to be significant predictors of the number of bat species/genera recorded (all $P > 0.05$), although time after sunset approached significance ($P = 0.053$) with a negative impact on bat activity throughout the evening. For the direct sampling data, the results of the ordinal logistic regression model reflect those above except the effect of time after sunset falls within the significance threshold ($P = 0.042$), with the number of bat species/genera recorded significantly decreasing with time after sunset (Figure 4.8; $\chi^2 = 4.15$, d.f. = 1, $P < 0.05$). With this model, the log odds of observing a greater number of species half an hour after sunset were 2.3 times higher than at two and a half hours after sunset.

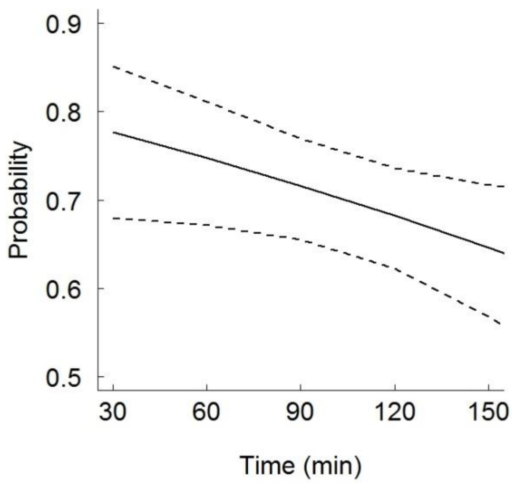

Figure 4.8: The probability of observing an increase of one bat species/genus with time after sunset.

Based on the predictions from the ordinal logistic regression model. The two hour transect period is shown. Dashed lines indicate 95% confidence intervals.

4.5 Discussion

Time expansion and direct sampling are currently the two most advanced methods available for recording the echolocation calls of bats. Both allow calls to be recorded without significant information loss, which is essential for subsequent analysis and the classification of bat species. There are, however, differences in these methods, and by simultaneously recording bat echolocation calls at spot checks using two different types of bat detector, we were able to compare the amount of bat activity recorded and the magnitude of road effects detected.

4.5.1 Differences between the datasets

A larger volume of data (over six times more) was collected using the direct sampling method than with time expansion, with a greater number of bat passes recorded per spot check. The detectors were calibrated prior to the study to ensure that the sensitivity and detection ranges were equal, and the results confirm that this was successful, as both methods recorded the presence of bats at a similar number of spot checks, and incidences where only one detector picked up calls were infrequent and did not differ between the devices. Species composition was also similar for both datasets. The difference in the amount of data collected can therefore be attributed to the techniques used by each method to deal with high frequency echolocation calls. Time expansion results in a loss of sampling time as detected calls are played back at a slower speed for recording. With a time expansion factor of ten, the detector will take 1.1 seconds to detect and playback 0.1 seconds of ultrasound, resulting in only 9.1% of the available time being sampled (Parsons *et al.* 2000). With direct sampling, however, recording is continuous with no breaks in sampling time resulting in a greater number of bat calls being recorded. If bat activity was constant throughout the ten minute spot check, we would therefore expect the direct sampling method to record ten times more activity than the time expansion method. We recorded on average six times more activity per spot check with direct sampling, and this is likely due to the intermittent nature of the bat activity being recorded. We did not detect bat calls continuously throughout any of our spot checks, and all of the ten minute recordings contained quiet periods. Therefore, the loss of sampling time that occurred during playback with the time expansion method will not always have coincided with bat activity and resulted in a loss of data, but may have occurred during quiescent periods. There was also greater variance in the direct sampling dataset with an increase in high outliers. With time expansion methods, losses in sampling time limit the number of calls that can be recorded in a given time, imposing a restriction on the highest levels of bat activity that can be sampled. As direct sampling can record constantly, it can and did record higher levels of bat activity, producing a greater differentiation in activity levels.

4.5.2 Road effects

We modelled both datasets to investigate the impact of the road on bat activity and whether the detection of this effect differs between sampling techniques. GEE models for both datasets revealed a negative impact of the road on total bat activity but the magnitude of the effect was predicted to be three times greater for the data collected by direct sampling. There could be several reasons for this difference. As discussed above, the limited sampling time available with time expansion methods may impose a restriction on the highest number of bat calls that can be recorded in a given time producing a decreased differentiation in activity levels. For the same reason, outliers are likely to be missed in the time expansion recordings, and as there are few high outliers in comparison to low outliers in this study, missing these may result in the road effect being reduced. Also, the results from the time expansion recordings will be more variable depending on whether sampling losses coincide with busy or quiet periods of bat activity, which may cause the road effect to vary each time the study is repeated. Further data would need to be collected to investigate these differences further, but it is clear that the direct sampling method produces more accurate and complete datasets with more resolving power for the effects that we are testing for.

4.5.3 The effect of time and habitat

Time after sunset, which only approached significance for predicting bat diversity with the time expansion data, became a significant variable when analysing the direct sampling data. The effect of time on bat diversity is not unexpected. We found that time after sunset had a negative impact on bat activity in our study in Chapter 2, and this is likely to reflect greater mobility after emergence before bats settle to forage at their regular sites or return to night roosts later in the evening (Hayes

1997). This effect was only just significant and potential bias was accounted for by performing transects in opposite directions. However, the observed increase in significance of this variable when analysing the direct sampling data shows that this data collection technique may enhance the ability to detect subtle changes in bat activity not possible with the limitations of time expansion methods.

Habitat type did not have a significant effect on bat activity or diversity for either dataset which may be due to the high quality habitat found consistently along transects by the road, although poor weather conditions must also be considered (this is discussed in Chapter 3).

4.5.4 Limitations and implications

Although time expansion methods can be useful to provide a relative measure of bat activity, the loss of sampling time incurred results in an incomplete picture of the activity being recorded, and may either reduce the ability to detect changes in bat activity or mask the magnitude of these changes. With more data available and continuous sampling, the direct sampling method is able to record all detectable bat echolocation calls during the sampling period creating a more accurate measure of bat activity, and the effects of influential variables. This has important implications for other studies. Bat detectors are often used to monitor the habitat preferences of bats (e.g. Vaughan *et al.* 1997; Russ & Montgomery 2003; Downs & Racey 2006; Smith & Racey 2008), or to assess how bats respond to threats (e.g. Patriquin & Barclay 2003; Kalcounis-Rueppell *et al.* 2007; Duchamp & Swihart 2008). The results of such studies should be interpreted with caution. Misinterpretation could lead to erroneous conclusions and inappropriate management. Failure to acknowledge and consider the limitations of acoustic tools were found to be common in a review of 46 papers from 1980 to 2001 that assessed habitat use by bats (Gannon & Sherwin 2004). Several recent studies have reported different results obtained using different types of bat detector and highlight the importance of taking these differences into account when interpreting results, and the need for standardized bat detector surveys (e.g. Adams *et al.* 2012; Skalak *et al.* 2012; Stahlschmidt & Brühl 2012).

Our own study in Chapter 2 used time expansion techniques to investigate the impact of another road on bat activity, and revealed negative effects with total activity increasing three fold between 0 and 1,600 m from the road. However, given the limitations of time expansion techniques revealed in this study, it is possible that these negative effects could be greater. Although this is speculation, it has important implications: our ability to detect the effect of the road may be constrained by the methods and technology available to us.

Although the merits of time expansion and direct sampling methods have been discussed (e.g. Jones *et al.* 2000; Parsons *et al.* 2000; Pettersson 2004), there are no previous studies which directly compare the use of these methods. Other methods have been compared in the past when new technology has been introduced with similar increases in accuracy being revealed as more advanced systems become available. For example, Johnson *et al*. (2002) found that recording bat calls from a frequency division bat detector directly to a computer, rather than to a tape recorder for transfer later, resulted in a higher quality dataset more than twice the size providing a more complete picture of the bat community being sampled. Fenton *et al.* (2001) found a significant difference in both numbers of bat echolocation calls and call characteristics when using two different techniques; time expansion and zero crossing period meter (another transformation technique to directly analyse calls). Adams *et al.* (2012) found that full spectrum recording detected significantly more calls than zero crossing techniques. Differences in the amount of data recorded have also been found between different brands of bat detector (Waters & Walsh 1994; Parsons 1996), and different triggering methods (Stahlschmidt & Brühl 2012).

There are very few studies in the literature that have used direct sampling methods to record bats. One study used direct sampling methods to detect differences in bat activity and species richness between organic and conventional farms, and used automated classification software to identify 89% of the bat passes recorded to species level (Wickramasinghe *et al.* 2003). The system used was less advanced and less convenient than that used in this study. There are also relatively few studies using time expansion techniques despite the technology being available since 1980.

4.5.5 Automated acoustic analysis

The use of automated acoustic identification software was essential to the direct sampling method in this study, as it allowed rapid and reliable analysis and classification of the large numbers of bat calls in our recordings. The automated software performs almost five times faster than playback in real time and can be left to run attended (Scott 2012). It also allows for the reliable identification of all UK bat species using machine learning algorithms, which is not possible with manual techniques (although this feature was not fully exploited for this study). Similar automated techniques have been tested in other studies with high rates of classification accuracy. For example, in one study many European bat species were identified using artificial neural networks to a median accuracy level of 84% (Walters *et al.* 2012), but classification of *Myotis* species was poor. In another, correct classification rates using ensembles of neural networks were as high as 91 to 100% for species that are difficult to distinguish such as *Myotis* (Redgwell *et al.* 2009). These automated techniques offer many advantages over manual analysis that can be slow, laborious, and error prone (Jennings *et al.* 2008), and not feasible for the large quantity of data produced by direct sampling.

4.5.6 Conclusions

Time expansion methods for recording bat activity result in significant losses in sampling time that limit the amount of data that can be collected and may reduce the accuracy and resolving power to detect effects that are being tested for. Continuous full spectrum recording of echolocation calls by direct sampling teamed with fast automatic call classification methods creates an advanced, efficient, more accurate package for analysing bat echolocation calls, revealing patterns in bat activity and measuring the density of bat populations, and will greatly enhance future studies.

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Chapter 5: Do bat gantries and underpasses help bats cross roads safely?

5.1 Abstract

Major roads can reduce bat abundance and diversity over considerable distances. To mitigate against these effects and comply with environmental law, many European countries install bridges, gantries or underpasses to make roads permeable and safer to cross. However, through lack of appropriate monitoring, there is little evidence to support their effectiveness. Three underpasses and four bat gantries were investigated in northern England. Echolocation call recordings and observations were used to determine the number of bats using underpasses in preference to crossing the road above, and the height at which bats crossed. At gantries, proximity to the gantry and height of crossing bats were measured. Data were compared to those from adjacent, severed commuting routes that had no crossing structure. At one underpass 96% of bats flew through it in preference to crossing the road above. This underpass was located on a pre-construction commuting route that allowed bats to pass without changing flight height or direction. At two underpasses attempts to divert bats from their original commuting routes were unsuccessful and bats crossed the road at traffic height. Underpasses have the potential to allow bats to cross roads safely if built on pre-construction commuting routes. Bat gantries were ineffective and used by a very small proportion of bats, even up to nine years after construction. Most bats near gantries crossed roads along severed, pre-construction commuting routes at heights that put them in the path of vehicles. Crossing height was strongly correlated with verge height, suggesting that elevated verges may have some value in mitigation, but increased flight height may be at the cost of reduced permeability. Green bridges should be explored as an alternative form of mitigation. Robust monitoring is essential to assess objectively the case for mitigation and to ensure it is effective.

5.2 Introduction

Recent research shows that major roads can have a negative impact on bats. In Chapters 2 and 3 we found declining bat activity and diversity in proximity to a major road, with the scale of the impact indicating a barrier effect. Studies of *Myotis bechsteinii* also provide evidence for a barrier effect with contracted foraging areas and reduced reproductive success in proximity to a road (Kerth & Melber 2009). Road avoidance behaviour has been observed in commuting bats (Zurcher *et al.* 2010; Bennett & Zurcher 2013), and street lighting (Stone *et al.* 2009; Stone *et al.* 2012) and traffic noise (Schaub *et al.* 2008; Siemers & Schaub 2010) reduce foraging activity and success. Numerous studies show that bats are killed on roads by collision with vehicles e.g. (e.g. Lesinski 2007; Gaisler *et al.* 2009; Russell *et al.* 2009; Lesinski *et al.* 2010). Roadkill is hard to quantify due to the difficulty of finding carcasses (Slater 2002; Santos *et al.* 2011), but low reproductive rates make bats particularly vulnerable to elevated adult mortality e.g. (e.g. Papadatou *et al.* 2011).

Roads are detrimental to a wide range of animals (reviewed by Trombulak & Frissell 2000; Fahrig & Rytwinski 2009; Benítez-López *et al.* 2010). Crossing structures, both under and over roads, have been built in an attempt to maintain connectivity across the landscape, and numerous studies report use of these structures by mammals and reptiles (e.g. Clevenger *et al.* 2001; Ng *et al.* 2004; Olsson *et al.* 2008; Grilo *et al.* 2009). However, the use of a mitigation feature, the widely accepted criterion for success, does not make it effective. To be effective it must play a significant role in maintaining local population sizes. Evidence for a small, unspecified proportion of individuals using a structure to cross a road is not evidence for effective mitigation if a greater proportion crosses the road unsafely, is forced to reduce home range size or has to make longer journeys to find an alternative route. Reviews of mitigation techniques for a wide range of animals report that studies assessing use are typically qualitative (Corlatti *et al.* 2009; Glista *et al.* 2009). In one such review, only two out of 123 studies were able to conclude a positive effect of mitigation at the population level (Van Der Ree *et al.* 2006).

European bats are protected by EU and national law (see Chapter 1 for details). Legally required mitigation measures on road developments usually take the form of crossing structures to maintain linear elements in the landscape that bats rely on for commuting. The use of wire bat bridges or 'gantries' is becoming increasingly common: at least eight have been built in the UK in the last five years and six more are planned for the A11 in Norfolk (Highways Agency 2008; O'Connor *et al.* 2011). However, there are no published data regarding the effectiveness of these structures. Recent reviews of case studies of bat mitigation in the UK found that most reports were at best qualitative and inconclusive (Altringham 2008; O'Connor *et al.* 2011). Green bridges, underpasses and culverts have been installed across Europe with potential use as a wildlife passage frequently being an unintended or secondary function. Most of the studies reporting their use by bats are unsuited to quantitative analysis, or fail to address the important distinction between use and effectiveness (e.g. Bach *et al.* 2004; Bach & Muller-Steiss 2005; Lambrechts *et al.* 2006). Seven bat species were caught flying through motorway underpasses in Germany, but when activity levels were compared with sites in the surrounding forest, only *Barbastella barbastellus* and *Myotis nattereri* were caught significantly more often in the underpasses, suggesting their effectiveness as crossing structures may be species-specific (Kerth & Melber 2009). The use of underpasses by at least six bat species was also reported in Ireland, with the tendency to fly through the underpasses rather than over the road being related to the degree of clutter-adaptation of a species (Abbott *et al.* 2012).

Our aim was to examine whether road crossing structures built for bats (or considered suitable for bats) are not only used but, moreover, are effective in guiding a significant proportion of bats safely over or under roads. The ideal study would determine the effectiveness of the structures in maintaining local bat population sizes, but this requires pre-construction data, which do not exist. We therefore studied their effectiveness in protecting crossing bats by reducing the risk of collision mortality. We studied underpasses, the most common wildlife crossing structure in Europe and North America, and wire bat gantries, bridge-like structures designed to guide echolocating bats over the road (see method for a detailed description). These are currently favoured in the UK and are also being built in other parts of Europe.

5.3 Methods

5.3.1 Study sites

All four study sites were located in northern England: three roads in Cumbria (A590, A595 and A66), and one in Northumberland (A69). All sites were located in rural lowland used primarily for agricultural grazing, with linear elements such as hedgerows, dry stone walls and tree lines providing connectivity for bats (Limpens & Kapteyn 1991; Verboom & Huitema 1997). The importance of all sites as bat foraging and commuting routes was established during pre-construction environmental impact assessment (O'Connor *et al.* 2011), but methodological differences and inadequate data in these assessments prevented comparison with this study. All roads were built to bypass nearby settlements with traffic volumes of 12,000 – 17,000 vehicles per day (Cumbria County Council 2011; Department for Transport 2011). All bat gantries were of similar design: two wooden or metal pylons erected at either side of the road with 2 or 3 pairs of wires spanning the road between them (approximately 20 m on two lane roads and 30 m on four lane roads), with plastic spheres at intervals of approximately 2 m, at a height of 6 - 9 m, and width of 2 m (see Figure 5.1 for example). They are presumed to act as linear features that will guide echolocating bats across roads above traffic height. At each gantry or underpass, we compared the number of bats using the structure with those crossing unsafely over the road. Where possible, we also compared crossing activity at the gantries and underpasses to that at adjacent or nearby severed but unmitigated commuting routes (as detailed below). The only sites we were unable to compare to nearby commuting routes were underpass B on the A590 and the A69 gantry, as explained below.

Figure 5.1: Photograph of a typical bat gantry.
The A590 bypass, Cumbria, UK.

5.3.1.1 The A590 High and Low Newton Bypass

The A590 High and Low Newton Bypass (Figure 5.2), opened in April 2008, is a 3.8 km dual carriageway in the Lake District National Park. Two underpasses, a bat gantry and two severed but unmitigated pre-construction commuting routes were studied. Underpass A (30 m length x 6 m width x 3 m height) carries a bridleway beneath the road (Figure 5.3). It is located near to (but not on) a known commuting route, but trees and shrubs were planted along 200 m of the road in an attempt to divert bats from the unmitigated commuting route (on a severed tree-line to the north) that we also surveyed for comparison (See Figures 5.4 & 5.5). Underpass B (30 m length x 6 m width x 5 m height, 500 m south of A) was built to carry a hedgerow-lined minor road, a known commuting route (Figure 5.6). There were no other previous commuting routes in close proximity for comparison to this underpass. The bat gantry, approximately 1000 m further south, crosses the road at a known commuting route along a severed hedgerow (Figure 5.7). We also surveyed a second unmitigated commuting route on a severed hedgerow 400 m north of the gantry, where the road now lies in a cutting up to 20 m deep (Figure 5.8).

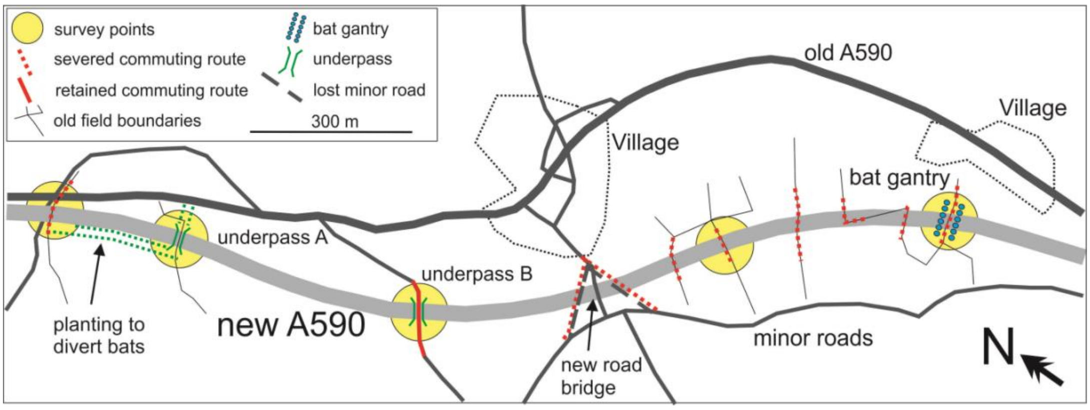

Figure 5.2: Map of the study sites on the A590.

Figure 5.3: Photographs of underpass A on the A590.

Both taken from the east.

Figure 5.4: Photographs of an unmitigated severed bat commuting route on the A590 near underpass A.

A) Taken from the west looking across to the severed tree line, B) taken from the east.

Figure 5.5: Photograph of a treeline planted to divert bats from the commuting route on the A590 to Underpass A.

Photo taken approximately two years after planting, on the western verge looking south.

Figure 5.6: Photographs of underpass B on the A590.

A) Taken from the west, B) from the east.

Figure 5.7: Photograph of the bat gantry on the A590.

Taken from the south-east.

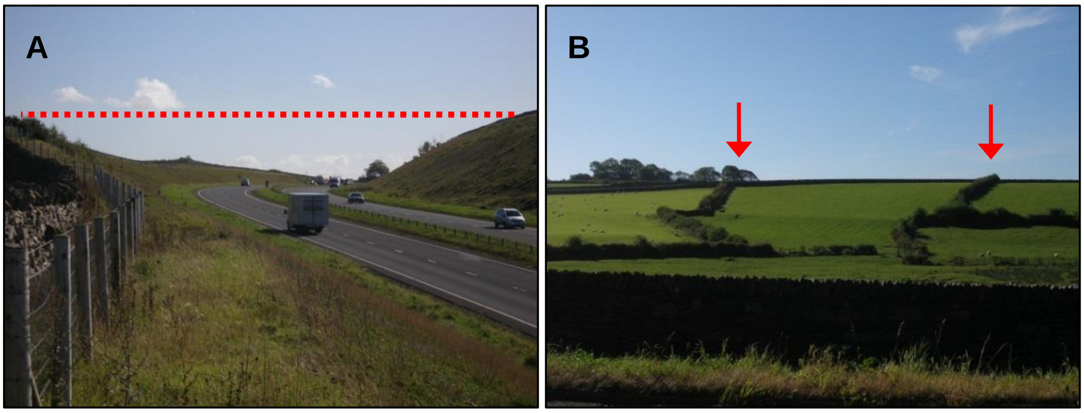

Figure 5.8: Photographs of severed bat commuting routes on the A590 near the bat gantry.

A) An unmitigated severed commuting route (marked in red) over the road cutting, photo taken from north-east, B) hedgerows leading up to the east embankment of the road and severed by the A590 in the cutting (marked by arrows).

5.3.1.2 The A595 Lillyhall to Parton Improvement

The A595 Lillyhall to Parton Improvement, opened in December 2008, is a 5.1 km dual carriageway. A bat gantry was installed where the bypass bisected woodland (Figure 5.9). We surveyed this gantry and an unmitigated commuting route 90 m to the north where a hedgerow was severed by the road (Figure 5.10).

Figure 5.9: Photograph of the bat gantry on the A595.

Taken from the north-east.

Figure 5.10: Photographs of an unmitigated severed commuting route by the A595 bat gantry.

Commuting routes marked in red, A) taken from the south west, B) taken from the west side to the severed hedgerow.

5.3.1.3 The A66 Stainburn and Great Clifton Bypass

The A66 Stainburn and Great Clifton Bypass, opened in December 2002, is a 4.2 km three-lane carriageway, bisecting a 30 m wide strip of mature woodland. The gantry (Figure 5.11) is located at the western edge of the wood 15 m from the pre-construction commuting route, a bridleway within the wood (Figure 5.12). We surveyed both the gantry and the pre-construction commuting route. An underpass

(15 m length x 5 m width x 2.5 m height; Figure 5.13) was built at the eastern edge of the wood to carry a small stream, and its use by crossing bats was also investigated.

Figure 5.11: Photograph of the bat gantry on the A66.

Taken from the south-west.

Figure 5.12: Photographs of the original severed commuting route by the bat gantry on the A66.

A) Taken from the north, commuting route marked in red, B) the bridleway of the original commuting route through the woodland on the north side of the road.

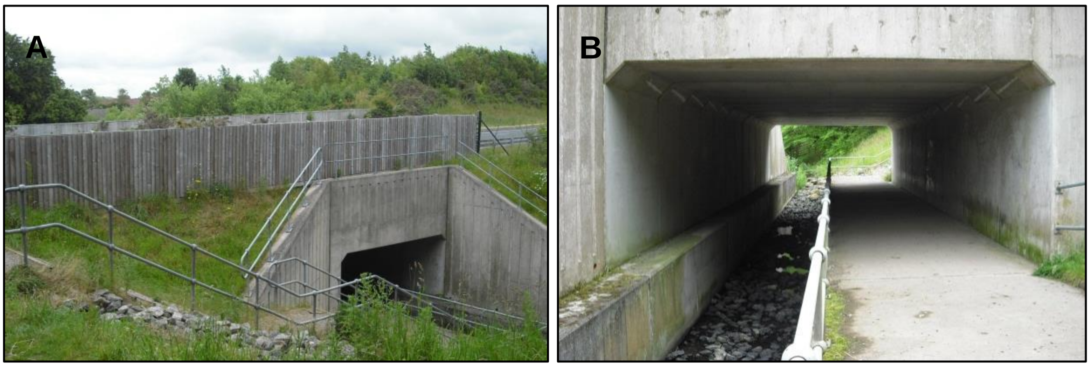

Figure 5.13: Photographs of the underpass below the A66.

A) Taken from the south side at road level, B) taken from the north side at underpass level.

5.3.1.4 The A69 Haydon Bridge Bypass

The A69 Haydon Bridge Bypass, opened in March 2009, is a 2.9 km two-lane carriageway. A bat gantry was constructed at the site of a bat flight line where the road severed a hedgerow (Figure 5.14). In pre-construction surveys, minimal bat activity was recorded on all potential commuting routes within 1 km, with the exception of Gee's Wood 800 m east, where the new road bridged a 100 m wide, 10-20 m deep wooded valley with a stream. We therefore conducted surveys at the gantry only.

Figure 5.14: Photograph of the bat gantry on the A69.
Taken from the south verge looking west.

5.3.2 Survey methods

Surveys were conducted in June and July, on the A590 in 2010, and all other sites in 2011. Ten 90 min surveys were completed at each crossing point, five commencing at sunset and five starting 90 min before sunrise. Only the five dusk surveys were conducted on the A69 due to low activity levels at dawn. Surveys were conducted on warm, still, dry nights to avoid weather dependent variation in bat activity.

At each crossing point an observer was positioned on the verge either side of the road, equipped with a Pettersson D240x broadband bat detector (www.batsound.com) and a solid state recorder (Edirol R-09HR, www.edirol.com) set up to automatically detect and record bat echolocation calls (100 ms time expanded to 1 s and recorded in mp3 (320 kbps) format). Since all events were "time-stamped", observations of crossing bats were later matched to echolocation call recordings for species identification. A Pettersson D500x (www.batsound.com) bat detector (suitable for automated logging) was also placed in the central reservation when one was present to increase the chances of detection and aid species identification. Both detectors provide recordings that preserve all essential frequency and amplitude information of the echolocation calls, making them the most appropriate choice for species identification. Bats recorded but not observed were excluded, although this was rare. Two observers were used to maximise observations and ensure crossing bats were not missed. All equipment was time synchronised and observers conferred via two way radios. Flight height, direction, distance from the gantry and time of crossing were recorded for each bat. Records were later combined and duplicates removed. Measured points of reference were used to estimate heights and distances to the nearest metre. The bat gantry, fencing and road signs were used for vertical references, and road markings and crash barrier posts provided horizontal reference points. A clear point of reference was always in view and estimations were made without difficulty. Flight height was recorded over the road, with the majority of bats (87%) crossing at constant heights. For those bats which altered their flight height during crossing (8% decreased height and 4% increased) the lowest flight height over the road was recorded. To corroborate observations night vision digital video cameras (Sony Nightshot DCR-SR75E and DCR-SR35, www.sony.co.uk) were set up on each verge facing the gantry or commuting route over the road, alongside heterodyne bat detectors used to indicate presence on the recordings (Batbox III, www.batbox.com) and infrared lights. However, these were found to be unnecessary with visual observations providing sufficient information.

At the underpasses, these methods were repeated on the road above and an additional observer with the same equipment was positioned at one end of the underpass below. Infrared lights were used to illuminate the underpass, and a night scope (Dedal generation 2, www.nightvision.ru) was used to aid observations. A Pettersson D500x bat detector (www.batsound.com) was placed in the centre of the underpass to aid in species identification.

5.3.3 Species identification

Batsound Pro software (www.batsound.com) was used to identify species from sonograms of their calls (Parsons & Jones 2000). In most cases, *Myotis* and *Nyctalus* were identified only to genus because of similarity in call structure (Parsons & Jones 2000). *Myotis nattereri*, *M. mystacinus*, *M. daubentonii* and *M. brandtii* are widespread in the area (Bellamy *et al.* 2013). *Nyctalus noctula* is widespread, and *N. leisleri* is rare. However, *Nyctalus* data were not analysed as bats flew at heights greater than 15 m over the road and commuting activity was low at most sites. A small proportion (<5%) of *Pipistrellus* calls was classified only to genus level, because of the overlap of call parameters of *P. pipistrellus* and *P. pygmaeus*. *Plecotus auritus* was also present, but will have been under-recorded because of its low intensity echolocation call (Parsons & Jones 2000). Species identification was not reliable for 30% of crossing bats due to noise or low intensity recordings. These records were therefore omitted for species specific analyses. All records (excluding *Nyctalus*) were used in all other analyses.

5.3.4 Definitions

'Safe' and 'unsafe' crossing heights were defined as being greater and less than 5 m above the road surface respectively. The maximum height for heavy goods vehicles in the UK is 4.95 m (The Road Vehicle (Construction and Use) Regulations 1986). Bats crossing the road below 5 m are therefore at risk of collision.

Two estimates of 'use' of the gantry were defined: bats crossing the road within 2 m or 5 m of the gantry at a safe height. These definitions are based on observations from the literature: *Myotis mystacinus* commuting at dusk from a roost to a foraging area flew 0.3 - 1.7 m from a hedgerow, with the greatest distances recorded only at irregularities in the hedge structure (Holderied *et al.* 2006). Commuting *M. daubentonii* flew 3.2 - 5.8 m from a forest edge and 2.1 - 4.5 m from a wall (Schaub & Schnitzler 2007).

5.3.5 Data analysis

We have provided statistical analyses, but in some cases, whether or not a particular result was statistically significant contributed little towards assessing the effectiveness of the crossing structures. For example, even if significantly more bats cross a road safely than unsafely, the impact on population trends ultimately depends on the proportion of the population that is killed in collisions. Statistical analyses were carried out using R (R Development Core Team 2006). Wilcoxon signed ranks tests used the function *Wilcoxsign_test* from the package *coin* (Hothorn *et al.* 2008) to compare activity per survey (n = 5 for A69, n = 10 for all other sites) between underpasses and the road above and between bats crossing at gantries and at unsafe heights below. Each survey was treated as independent. Although activity was generally lower at dusk, there was no observable variation in the behaviour of crossing bats between dusk and dawn and so the data were combined. Some individuals may have been recorded several times during surveys but this was unavoidable, and each crossing event was considered to be important regardless of this. The relationship between flight height and verge height was investigated using Spearman's rank correlation (*cor.test*) and comparisons were made between species using Kruskal - Wallis tests (*kruskal.test*) and pairwise Wilcoxon rank sum W tests (*wilcox_test* function, package *coin*) with Bonferroni corrections. On the A66, observations were made across the entire 30 m section of severed woodland that included both the gantry and the severed commuting route. The heights and positions of all crossing bats were used to generate a kernel estimate of crossing intensity, using the *density* function in the *spatstat* package (Baddeley & Turner 2005).

5.4 Results

5.4.1 Underpasses

At underpass A on the A590, activity was low (Table 5.1, Figure 5.15A), but 69% of bats preferred to fly over the road rather than use the underpass (Z = -2.39, *P* = 0.03). Of bats crossing the road, 88% did so at unsafe heights. *Pipistrellus pipistrellus* and *P. pygmaeus* were detected in the underpass. *P. pipistrellus*, *Myotis* and *Plecotus auritus* were detected flying over the road. Over the same period, more bats crossed the road at the nearby unmitigated, severed commuting route (Table 5.1, Figure 5.15A), 58% at unsafe heights. Most were *P. pipistrellus* and *P. pygmaeus*, approximately half crossing below 5 m. Four of the five *Myotis* detected crossed below 5 m. No bats were observed flying along the planted diversion to the underpass, but observers were only able to monitor this where it left the original commuting route.

Activity levels were higher at underpass B than at A (Table 5.1, Figure 5.15B) and many more bats (96%) used the underpass than flew over the road above at unsafe heights (Z = 2.80, *P* = 0.002). *P. pipistrellus*, *P. pygmaeus* and *Myotis* were all detected both in the underpass and over the road.

Activity in the underpass below the A66 was low (Table 5.1, Figure 5.15C), with only 4% of bats crossing through it, in comparison to 60% crossing at unsafe heights over the road above (Z = 2.80, *P* = 0.002). *P. pipistrellus, P. pygmaeus* and *Myotis* were detected over the road and in the underpass.

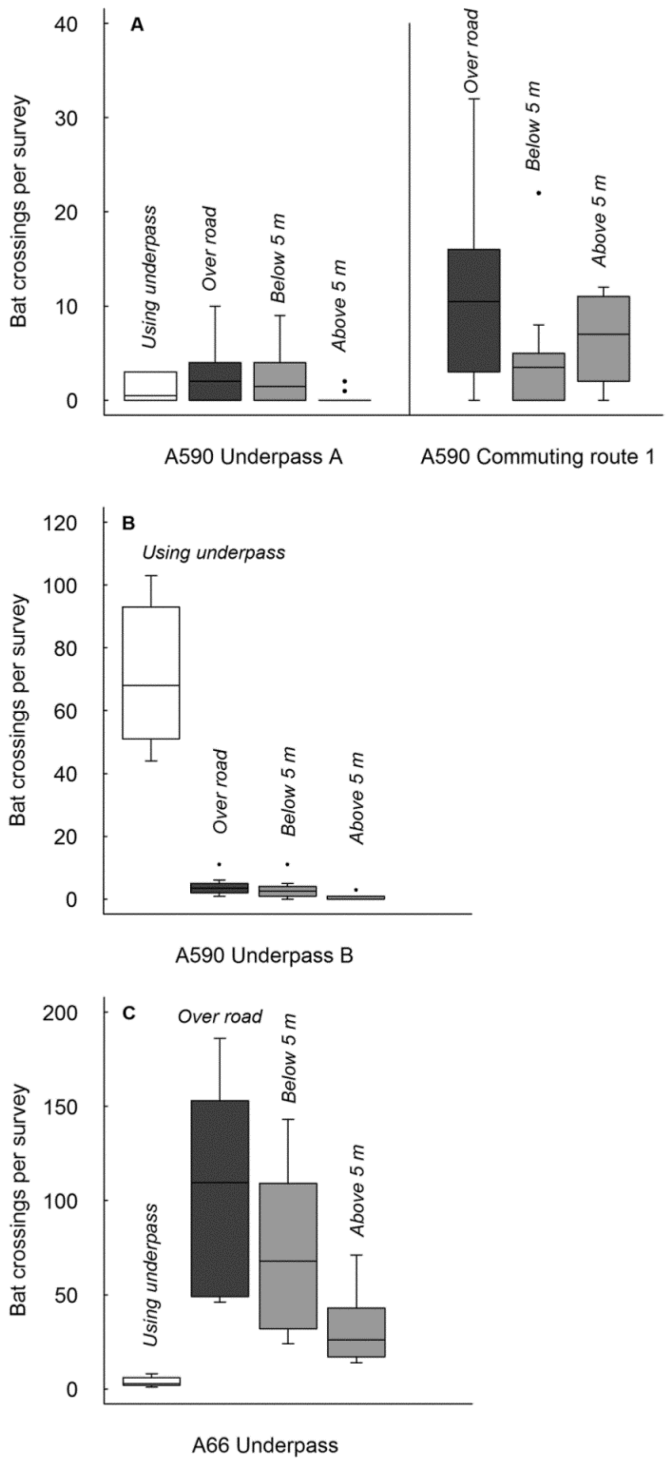

Figure 5.15: Boxplots of the number of bats crossing per survey at each underpass.

Shows median with upper and lower quartiles for the number of bats crossing per survey (n = 10) at each underpass (numbers crossing using underpass, over the road above and at safe and unsafe heights over the road), and at the unmitigated commuting route on the A590 which was diverted to underpass A (numbers crossing over the road and at safe and unsafe heights).

Table 5.1: The crossing behaviour of all bats from all surveys for each study site.

(NB the number of bats crossing at safe heights at the gantries includes those ‘using’ the gantry).

Road	Site	Total crossing	‘Using’ gantry (within 2 m)	‘Using’ gantry (within 5 m)	Using underpass	Unsafe height over road (< 5 m)	Safe height over road (> 5 m)
A590	Underpass A	36	-	-	11	22	3
	Commuting route 1	113	-	-	-	65	48
	Underpass B	904	-	-	864	32	8
	Bat gantry	104	11	31	-	43	61
	Commuting route 2	19	-	-	-	0	19
A595	Bat gantry	96	1	6	-	81	15
	Commuting route	77	-	-	-	72	5
A66	Combined survey area (Bat gantry, Commuting route & underpass)	1117	24	100	39	751	327
A69	Bat gantry	65	5	27	-	10	55

5.4.2 Bat gantries

At all sites, few bats crossed using the gantry (Table 5.1, Figure 5.16). At the A590 gantry (Figure 5.16A), four times as many (41%) crossed the road at unsafe heights as crossed within 2 m of the gantry (11%; Z = 2.61, *P* = 0.008), and 1.4 times as many as crossed within 5 m of the gantry (30%; Z = 1.49, *P* = 0.15). At the A595 gantry (Figure 5.16B), far more bats (84%) crossed the road at unsafe heights than flew within 2 m (<1%; Z = 2.81, *P* = 0.002) or 5 m (6%; Z = 2.81, *P* = 0.002) of the gantry. At the A69 gantry (Figure 5.16C), more bats crossed the road at unsafe heights (17%) than flew within 2 m of the gantry (8%; Z = 1.17, *P* = 0.31), but fewer bats crossed at unsafe heights compared to those flying within 5 m of the gantry (42%; Z = -2.14, *P* = 0.06).

At the A66 survey area (including both the gantry and the pre-construction commuting route, Figure 5.16D), far more bats (70%) crossed at unsafe heights, than flew within 2 m (2 %; Z = 2.81, *P* = 0.002) or 5 m (9%; Z = 2.81, *P* = 0.002) of the gantry. The kernel density estimation for the A66 (Figure 5.17) shows a high concentration of bats crossing at unsafe heights centred at the unmitigated pre-construction commuting route, and low activity around the gantry.

On the A595 the number of bats crossing at the nearby unmitigated, severed commuting route (Figure 5.16B) was comparable with that crossing in the vicinity of the gantry, and 94 % of bats crossed at unsafe heights.

At the unmitigated, severed commuting route near the gantry on the A590 foraging activity of *P. pipistrellus* was observed during all surveys on the western side of the road, but only 19 bats crossed over 10 surveys, all at safe heights. Although other severed commuting routes (shown in Figure 5.2) were not surveyed, significant crossing activity was not observed during reconnaissance.

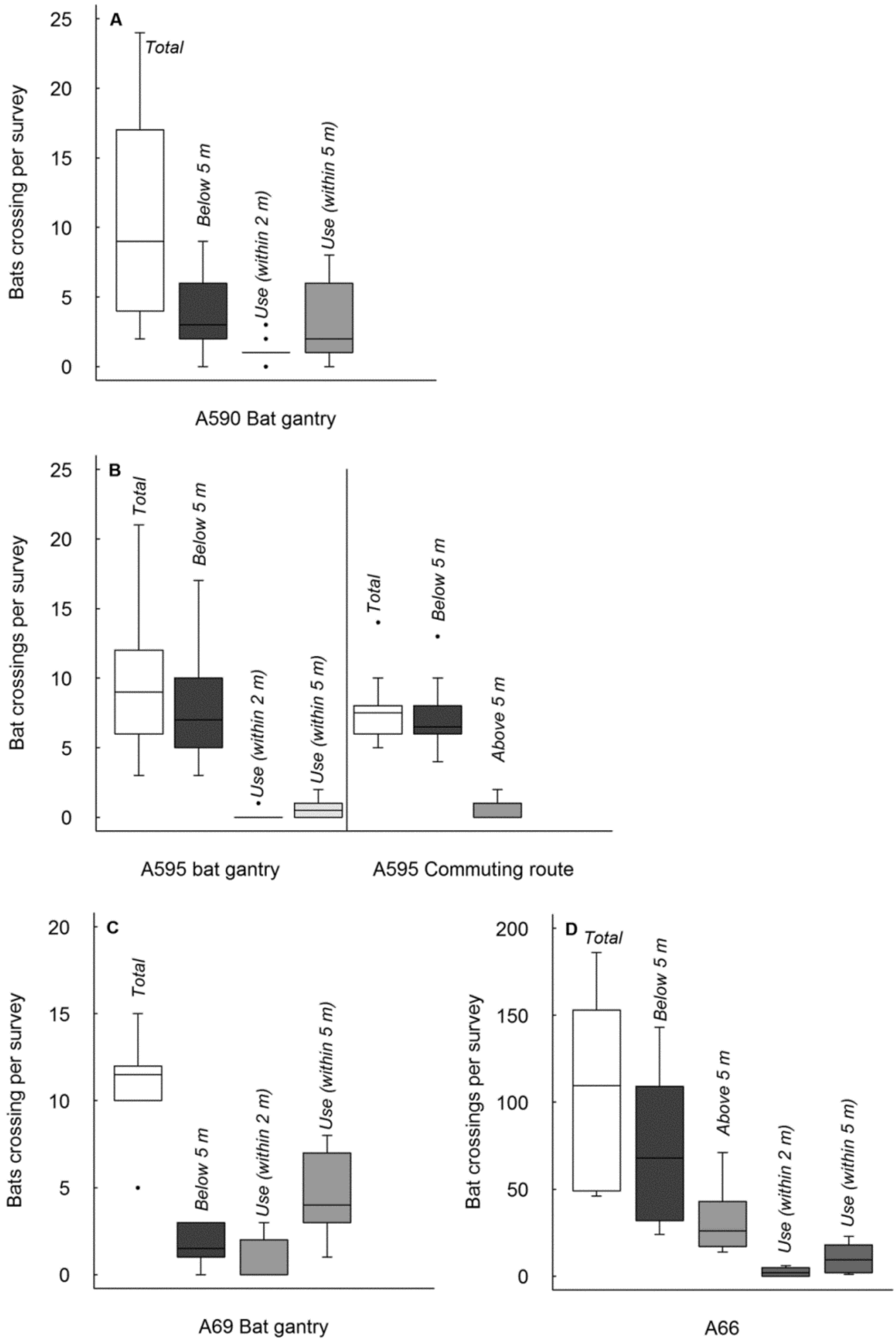

Figure 5.16: Boxplots of the number of bats crossing per survey at each bat gantry.

Shows median with upper and lower quartiles of the number of bats crossing per survey (n = 10) at the four bat gantries, together with data on total number crossing, the numbers crossing at safe and unsafe heights, numbers 'using' the gantry according to both estimates (within 2 and 5m), and the numbers crossing at nearby, unmitigated, severed commuting route nearby.

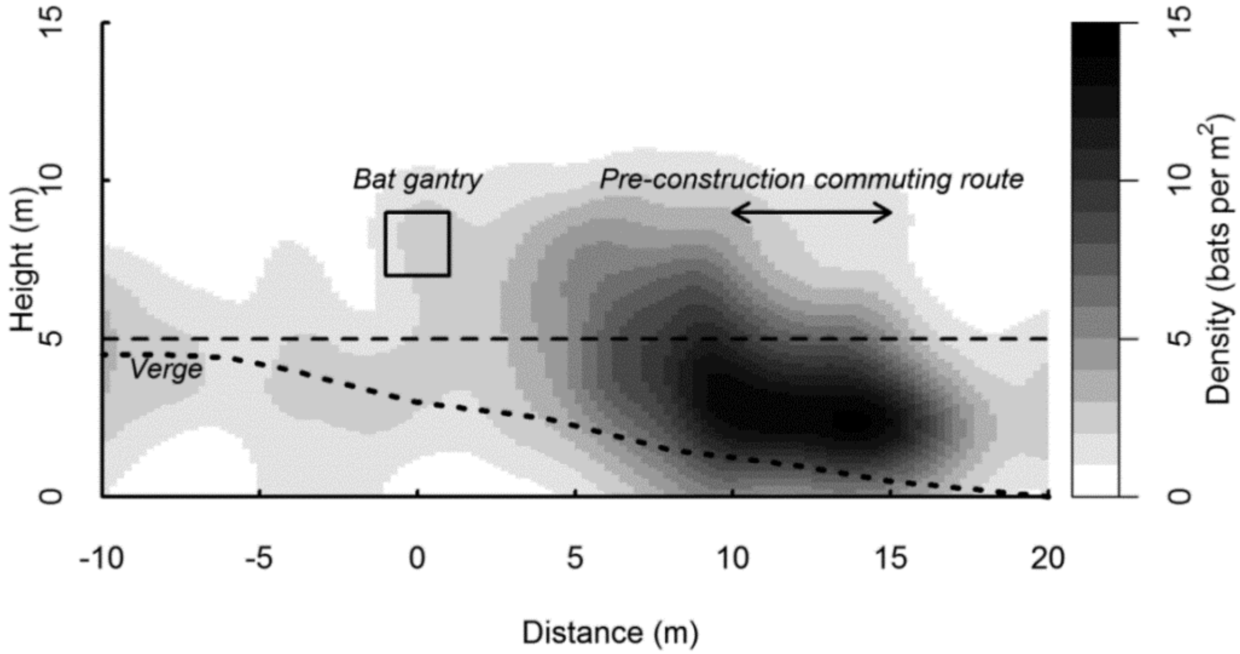

Figure 5.17: Kernel density estimation of crossing bats across the A66 site.

Gaussian kernel and bandwidth of 1 m used (n = 1078). The section of severed woodland at the A66 site is shown. The gantry is located at distance 0 m (height marked by square), and the pre-construction commuting route at 10 – 15 m. ‘Unsafe’ crossing heights are located below the dashed line. The dotted line marked verge shows the decrease in verge height above the road from left to right.

5.4.3 The influence of verge height

The mean crossing height of all bats across all sites (excluding underpasses) was positively correlated with verge height (estimated to nearest 0.5 m) at the point of crossing (Spearman's rank; r = 0.34, n = 1552, $P < 0.0001$). This correlation was significant at the species/genus level, with *Myotis* showing the strongest relationship (*Myotis*: r = 0.46, n = 55, $P < 0.001$; *P. pipistrellus*: r = 0.40, n = 284, $P < 0.0001$; *P. pygmaeus*: r = 0.34, n = 343, $P < 0.0001$). Crossing height above the height of the verge was found to vary between genera (Figure 5.18). No difference was found between the two *Pipistrellus* species (Wilcoxon rank sum; W = 47193.5, $P > 0.05$ after correction), but *Myotis* flew significantly lower than both *P. pipistrellus* (Wilcoxon rank sum; W = 5306.5, $P < 0.0005$ after correction) and *P. pygmaeus* (Wilcoxon rank sum; W =5935, $P < 0.0001$ after correction). Only three *P. auritus* were detected, and all crossed below the height of the verge at < 3 m over the road.

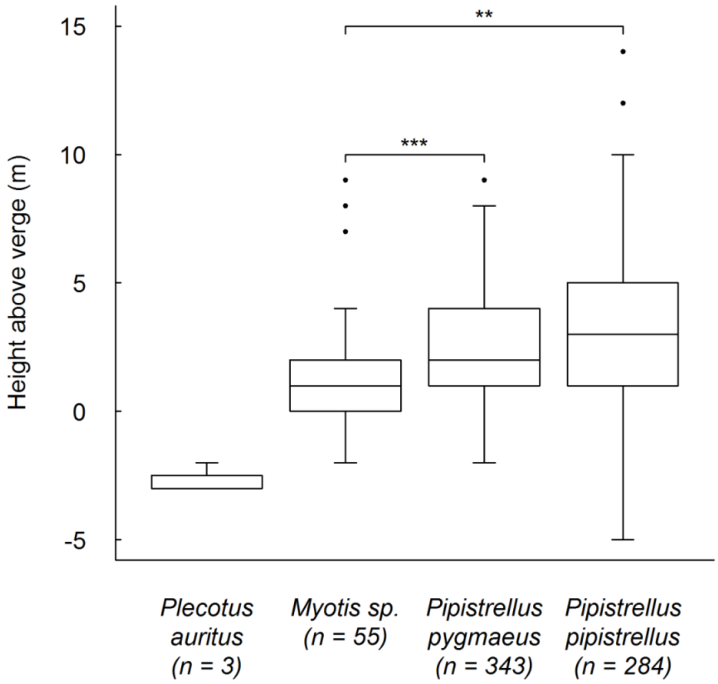

Figure 5.18: Boxplot of flight height above verge height of identified crossing bats at all sites.

Median with upper and lower quartiles and outliers. Significant differences shown for *Myotis* and *Pipistrellus* species ** $P < 0.0005$,*** $P < 0.0001$. Excludes underpass sites. Verges are elevated on either side of the road and are above road height, therefore negative values indicate bats flying across the road below the height of the verge.

5.5 Discussion

This is the first study to assess the effectiveness of road crossing structures for bats, by measuring the proportion of individuals that used these structures to cross safely. Although a limited study of such diverse structures cannot be definitive, we believe it demonstrates that some current practices are failing. We found no evidence that bats used gantries in preference to nearby, severed but unmitigated commuting routes. At all but one site (A69, where activity was low), the majority of bats crossed at unsafe heights, even in proximity to gantries. Of seven mitigation structures studied, only one underpass was effective in carrying the majority of bats safely across the road.

5.5.1 Underpasses

Underpass A on the A590, and the A66 underpass, are not effective mitigation measures: very few bats flew through them relative to the number crossing at unsafe heights over the road above, and in the case of underpass A, at an original commuting route nearby. Underpass B on the A590 showed high levels of use by commuting bats, with just 4% crossing at risk of collision mortality on the road above. This underpass is effective in allowing bats to cross the road safely. However, the lack of robust pre-construction population data makes it difficult to assess how effectively this underpass can protect bat populations. Even though a high proportion of bats use the underpass, if bat populations have declined since construction and the road acts as a barrier, then the underpass becomes ineffective. Nevertheless, underpass B preserved a pre-construction commuting route, with no necessity for commuting bats to alter their flight course or height. Although replication is needed, this shows that underpasses can be effective when built over existing commuting routes. This makes sense in the context of the high fidelity that bats show to their commuting routes (Racey & Swift 1985; Verboom & Spoelstra 1999; Senior *et al.* 2005). Underpass A and the A66 underpass were unsuccessful probably because they require commuting bats to alter their course and flight height. Both underpasses are also lower than underpass B, but several studies report bats flying through even smaller structures (e.g. Bach *et al.* 2004).

5.5.2 Bat gantries

Bats did not cross at gantries more than at unmitigated road crossings, and gantries did not effectively increase the height at which bats flew above the road. There was no evidence that bats were 'using' gantries by flying in close proximity to them, as they do along hedges (Holderied *et al.* 2006; Schaub & Schnitzler 2007).

These bat gantries are failing to perform the function for which they were built, even at well-established sites such as the A66, where the gantry has been in place for nine years and is only 10-15 m from the original commuting route. Although road kill counts were not performed, it is well documented that bats are killed on roads in high numbers (Lesinski 2007; Gaisler *et al.* 2009; Russell *et al.* 2009; Lesinski *et al.* 2010) and mortality may be high enough to be unsustainable (Altringham 2008).

5.5.3 Verge height

The strong correlation between verge height and the average crossing height of bats suggests that increased verge height may have some potential in raising flight height above traffic. This effect was found to vary between species: *Myotis* species were most sensitive to changes in verge height and flew closer to the verge than *Pipistrellus* species, as did the few *Plecotus auritus* observed. However, increased verge height generally widens the open terrain that must be crossed (since they are inclined away from the road, higher verges are usually wider, see Figure 5.8), which could deter some species from crossing, increasing the barrier effect. Very few bats crossed the road at the second unmitigated commuting route on the A590, where verges are 20 m high, and the width of the open space is 80 m. Similarly, in Germany, *Myotis bechsteinii* were observed to frequently fly over a two lane road with a connecting tree canopy, but not over a four lane motorway with a gap in the forest (Kerth & Melber 2009).

5.5.4 Habitat continuity

It has been suggested that crossing structures will be more effective if continuous with the vegetation on either side of the road (Russell *et al.* 2009). However, even though the A66 gantry is connected to mature woodland on either side and is only 10-15 m from the commuting route, it is still ineffective. Commuting bats use linear habitat elements not just for navigation, but also to obtain protection from predation and wind and as foraging microhabitats (Verboom & Huitema 1997; Verboom & Spoelstra 1999). More substantial structures that provide shelter and perhaps bear a closer resemblance to natural features are likely to be more successful, for example a planted green bridge that provides a continuation of hedgerow, or tree lines over the road. Green bridges, although built for other wildlife, are only just being considered as mitigation measures for bats, and evidence is still needed for their effectiveness. Ten species of bat were found to use green bridges in Germany, with higher use than conventional road bridges, but results focussed on bats using the structures and did not look at those crossing the road below (Bach & Muller-Steiss 2005). A simpler (but as yet untested) alternative that may be practical and effective on narrower roads is the ‘hop-over’: mature trees that overhang the road so that their crowns bridge the gap above the road (Limpens *et al.* 2005).

5.5.5 Species – specific effects

Nyctalus species do not appear to be adversely affected by roads. High foraging activity was observed over traffic at one site (A69), and small numbers of commuting *Nyctalus* were observed over the A590 at heights of over 15 m above the road. In other studies *Nyctalus* species have been observed flying high over roads with no recordings in underpasses (See Chapter 2, & Bach *et al.* 2004; Kerth & Melber 2009), and low incidences of collision mortality (Lesinski 2007; Gaisler *et al.* 2009). Roads have been found to have less of an impact on habitat use by other bat species that also forage in more open habitat, such as *Barbastella barbastellus* (Kerth & Melber 2009).

All other species detected in this study crossed at unsafe heights over the road. Differences in crossing heights were found between species, with *Myotis* species (and the three detected *P. auritus*) flying lower over the road than *Pipistrellus* species, increasing their vulnerability to collision mortality.

5.5.6 The effectiveness of the survey and monitoring process

The bat gantries and one of the underpasses were installed because they were believed to be on significant commuting routes. However, we found activity was low at all gantry sites with the exception of the A66. Either activity has greatly diminished post-construction, adding to the conclusion of mitigation failure, or the assessment of these sites as major commuting routes was perhaps flawed. The absence of robust pre-construction monitoring means that we cannot say which explanation is correct. This raises serious questions about the effectiveness of the survey, assessment, mitigation and monitoring process. Several of the structures we have shown to be ineffective were said to be working in the commissioned reports (O'Connor *et al.* 2011), using the criterion that bats were seen to use them. Are other aspects of the reports equally flawed? Limited resources are available for conservation and it is vital that they are used effectively. Failure to do so makes no contribution to conservation and alienates further those outside it who question the use of public funds on conservation, e.g. the recent spending of £0.5M on bat gantries (Daily Mail 2011; The Telegraph 2011).

5.5.7 Conclusions and recommendations

We assessed only a small number of mitigation structures, but the results are sufficiently striking that wider appraisal is essential if mitigation against road construction is to be effective. Wire bat gantries, of the type studied, should not be used, and attempts to divert original commuting routes should, if possible, be avoided. Underpasses built on existing commuting routes can be effective crossing structures, if commuting bats can maintain their original course and flight height. Further investigation into more substantial, natural crossing structures over roads, such as green bridges, and simpler options such as tree 'hop-overs', is needed. Unique aspects of individual sites, such as tree cover, hedges and topography must be exploited to make mitigation solutions as natural as possible and appropriate to the bat species present. Robust and comparable pre- and post-construction monitoring must be carried out that assesses more objectively the need for mitigation and its effectiveness.

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Chapter 6: General Discussion

6.1 The effects of roads on bats

We have shown that roads can have a dramatic, large scale negative impact on bat activity and diversity, which can be explained by a combination of a barrier effect and increased mortality due to collisions with traffic. Our results are supported by previous findings, such as the reduced reproductive success and smaller foraging areas of female *Myotis bechsteinii* in proximity to a road (Kerth & Melber 2009), numerous accounts of bat mortalities resulting from collisions with traffic (e.g. Lesinski 2007; Gaisler *et al.* 2009; Russell *et al.* 2009; Lesinski *et al.* 2010), road avoidance behaviour by bats (Zurcher *et al.* 2010; Bennett & Zurcher 2013), and the negative impacts of street lighting (Stone *et al.* 2009; Stone *et al.* 2012) and traffic noise on bats (Schaub *et al.* 2008; Siemers & Schaub 2010).

To reliably assess the effects of roads on bats, it is important that robust, standardised methods are used to produce comparable data and allow for quantitative analysis. Much of the previous work has not met these requirements as it has been done through ecological consultancy where environmental survey and monitoring is typically subjective and qualitative, and is conducted over an insufficient duration to allow reliable conclusions to be drawn. We have developed a robust and effective method to detect and measure the landscape level impact of roads on bats, and we propose that methods such as these should be adopted as a standardised procedure when assessing road effects. We have demonstrated the benefits of using the latest technology in acoustic data collection. Direct sampling methods allow a greater range and larger volume of bat echolocation calls to be recorded, improving accuracy, and in this case revealing a road effect of a greater magnitude than detected using time expansion methods. We also demonstrated the use of the latest automated identification software which allows rapid and accurate species classification of the large number of bat calls recorded by direct sampling (Scott 2012). In this study, we analysed most calls to the genus level for direct comparison with the time expansion data, but the software is capable of reliably identifying all UK species. We are currently re-analysing the data collected by direct sampling in Chapter 3 to the species level to provide more information about the species-specific effects of roads. We will also explore the interaction with habitat further by entering the species records into a Geographic Information System (GIS) alongside more detailed data on linear landscape features, such as the structural complexity of hedgerows (height, width, continuity, emergent tree cover) and the proximity to woodland edge. We recommend the use of direct sampling detection methods teamed with automated call classification software to provide a more efficient and accurate method, which is applicable not just to road developments but to any future echolocation studies of bat activity.

6.2 Mitigation

It is a requirement by law in many countries that developments affecting protected species have mitigation measures in place to negate any adverse impacts. For example, in the UK, a licence must be obtained from a regulatory organisation for developments affecting protected species, and developers must show that there will be no adverse effects on the population of the species in the long term, with adequate mitigation measures implemented to negate or compensate for any such effects (Council Directive 92/43/EEC; Natural England 2013). However, the effects of developments and the effectiveness of mitigation are rarely assessed objectively or quantitatively, and a lack of evidence for mitigation is common for all wildlife (Van Der Ree *et al.* 2006; Glista *et al.* 2009; Lesbarrères & Fahrig 2012).

6.2.1 Crossing structures

Wire bat gantries, of the design tested in this study, are ineffective and should not be built. We did not test other designs of bat gantry, but given the low proportion of bats that could be considered to be using gantries to cross roads safely in this study, small differences in design are unlikely to result in a significant increase in effectiveness. However, other designs of bat gantry should be tested, as it is important to build an evidence base for what does and doesn't work so that ambiguity is avoided and appropriate decisions can be made in the future for successful mitigation. We are being funded by Defra (Department for Environment, Food and Rural Affairs, UK Government) over the next two years to test the effectiveness of other currently used mitigation measures, including other types of bat gantry.

Attempts to divert bats should be avoided. Bats are known to be highly faithful to their flight routes (e.g. Bontadina *et al.* 2005; Frey-Ehrenbold *et al.* 2013), and this was supported by our results. At all sites, bats continued to fly along original commuting routes, often at traffic height, despite attempts to divert them to alternate crossing points with tree and hedge plantings. The only underpass that could be considered successful in helping bats to cross the road safely in this study was built on the exact location of a previous bat commuting route, and bats were not required to alter their flight height or direction to fly through it. This suggests that underpasses may have some potential as road crossing structures for bats, and the use of underpasses by bats has been demonstrated in previous studies (Bach *et al.* 2004; Boonman 2011; Abbott *et al.* 2012a). However, position and underpass dimensions may need careful consideration and further research at a range of underpass sites is required.

We tested two types of bat mitigation and further research is needed into other types of structure which may be effective for reducing the barrier effect of roads. As well as underpasses, we suggest research should focus on green bridges and 'hop-overs'. Green bridges provide a more substantial natural structure to guide bats over roads, and if built to incorporate original commuting features, such as hedgerows, it is possible that they will be effective. A study in Germany indicates that bats will use green bridges to cross roads (Bach & Muller-Steiss 2005), but assessment is still needed in terms of the proportions of bats using them and their effectiveness in maintaining local bat populations. 'Hop-overs' may also provide a simpler alternative where mature trees overhang the road creating a continuous canopy that bats may follow at a safe height above traffic (Limpens *et al.* 2005). We found a positive correlation between road-crossing height and the height of the roadside embankment (Chapter 2), and bats have been found to cross road gaps at greater heights where there is taller roadside vegetation (Russell *et al.* 2009). However, further research is needed as hop-overs may be ineffective for low-flying species.

6.2.2 Habitat Improvements

Our study also provides strong implications for habitat improvements as mitigation for bats by roads, as our results suggest that the negative effects of roads on bat activity and diversity are reduced in areas of well-connected high quality habitat. By improving existing bat habitat around roads and increasing connectivity between habitat patches, we may be able to reduce some of the adverse impacts of roads on bats. Such compensatory mitigation has been discussed widely in the literature (e.g. Darbi *et al.* 2009; Moilanen *et al.* 2009; Tischew *et al.* 2010) including some of the practical difficulties, such as the issues of land availability, conflict of interest, the establishment time of habitats, the difficulty in quantifying the amount of habitat to improve or replace, and the costs involved. There is little evidence for the effectiveness of compensation mitigation as many previous attempts have failed due to implementation issues such as poor compliance, goal setting and management (Tischew *et al.* 2010). However, there have been some successes for compensation mitigation for amphibians and birds (e.g. Petranka *et al.* 2003; Balcombe *et al.* 2005; Brown *et al.* 2012), and although it has not been tested for bats, they have been shown to respond positively to other types of habitat restoration (e.g. Menzel *et al.* 2005; Smith & Gehrt 2010). There is the potential for this type of mitigation to be successful for bats as well as other wildlife in a range of scenarios, but to be successful it will require careful planning and implementation.

6.2.3 An integrated approach

Although further research is required into the effectiveness of mitigation structures and habitat improvements, we suggest that an integrated approach should be used for mitigation. Compensation is often used as a final measure in a hierarchy of three planning concepts: avoidance, mitigation and compensation (e.g. Cuperus *et al.* 1999; Rundcrantz & Skärbäck 2003; Darbi *et al.* 2009). In the first instance, detrimental developments should be avoided. Where this is not possible, adverse impacts should be mitigated, and finally any remaining adverse impacts should be compensated. Cuperus *et al.* (1999) have suggested combining mitigation measures to increase road permeability, such as crossing structures, with habitat compensation on both sides of the road to address the adverse impacts of habitat loss, habitat degradation and the barrier effect. We suggest that this approach is used to mitigate against the negative impact of roads on bats (Figure 6.1), with the aim to: i) maintain connectivity between habitats severed by the road by installing effective crossing structures such as underpasses on original flight lines, ii) improve connectivity in the surrounding landscape, for example by planting or improving hedgerows and treelines between habitat patches, e.g. up to 1 km on either side of the road, and iii) improve existing habitat in the vicinity by restoring or planting woodland and/or wetlands.

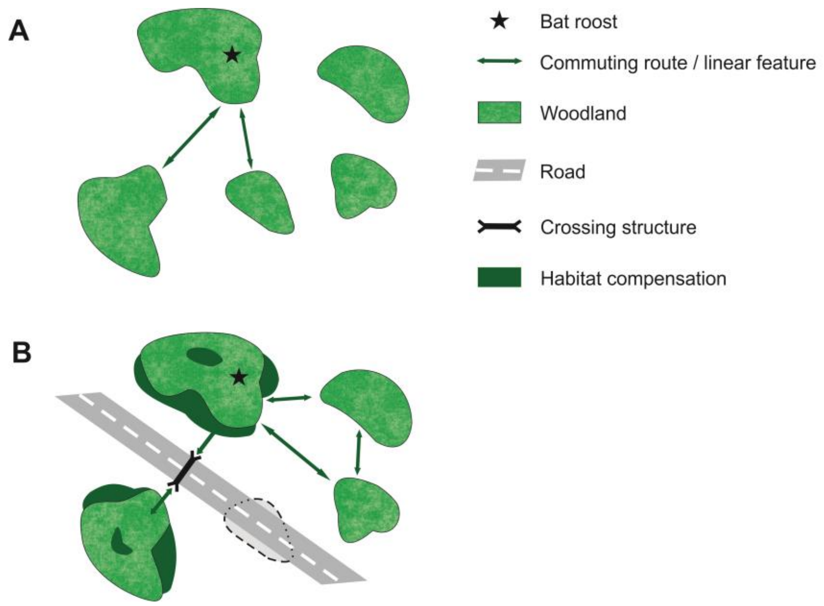

Figure 6.1: Mitigation and compensation for road effects.

A) Before road construction, B) after road construction with a mitigation crossing structure and habitat improvements (upgrading, enlarging and connecting). Adapted from Cuperus *et al.* (1999).

Although general principles for mitigation can be suggested, exact specifications must be tailored to each site and the bat species present, with solutions that minimise cost. The flight and foraging ecology of different bat species means that they may be affected differently by roads, and may have different responses to mitigation structures. For example, differences in flight heights linked to foraging ecology between species may affect the probability of collision mortality (Gaisler *et al.* 2009), and the degree of clutter adaption may affect the use of narrow culverts beneath roads by bats (Abbott *et al.* 2012b). Differences between sites will need to be given consideration on both the local and landscape level, and unique aspects of individual sites, such as tree cover, hedges and topography should be exploited to make mitigation solutions as natural and cost effective as possible. The amount of habitat to be improved or replaced will also differ between sites, and will depend on the location of roosts, commuting routes and foraging habitat.

6.2.4 Testing the effectiveness of mitigation measures

The aim of mitigation under European law is that it compensates for any adverse impacts of developments on the conservation status of protected species, so that population sizes are maintained in the long term (Council Directive 92/43/EEC ; Natural England 2013). There were limitations to our study of bat mitigation structures, which meant we could not assess the impact on bat populations. It was not possible to survey before and after road construction within the scope of this study, and comparable pre-construction data were not available. However, we designed a method which allowed us to quantitatively assess for the first time a fundamental requirement of bat mitigation structures; that they guide a significant proportion of bats safely across roads. There is an important distinction between our study and those that assess only the use of mitigation by an unknown proportion of individuals, which can produce misleading results. We have shown that at sites where bats can be considered to be using crossing structures, there may be a much greater proportion of bats crossing the road at unsafe heights below or at original commuting routes at risk of collision with vehicles. There may also be a proportion of bats approaching roads along commuting routes that veer away (e.g. Zurcher *et al.* 2010;

Bennett & Zurcher 2013), and are forced to seek out alternate routes or foraging habitats. All of these responses put local bat populations at risk, making mitigation ineffective. It is essential, therefore, that assessment of mitigation focuses on effectiveness rather than ‘use’ alone, which does not guarantee the survival of the whole population (Corlatti *et al.* 2009) or equate to conservation gain (Van Der Ree *et al.* 2006).

In the future, comparable pre- and post-construction monitoring should be conducted to assess mitigation, as even a large proportion of bats using a structure to cross a road safely may not be effective in maintaining local bat populations if the overall number of bats has already declined significantly since the construction of the road. This monitoring must be systematic and standardised in terms of survey effort, season, location, protocols and equipment (using methods such as those used in this study), to allow comparisons of bat activity and density to be made before and after road construction. The frequency and intensity of monitoring must also be sufficient to detect potential changes in bat activity despite the large amount of variation that is often inherent in ecological data. Surveys must be conducted over multiple nights to account for temporal variation in activity patterns between nights, as failure to do so can produce biased results (e.g. Hayes 1997; Fischer *et al.* 2009; Skalak *et al.* 2012). Monitoring must also be done in the long term (ideally ~ 10 years) as time lags can make demographic results slow to reveal themselves. Appropriate quantitative statistical analysis of the data is essential for objective appraisal, rather than the qualitative and anecdotal presentation and subjective interpretation that are currently common in the industry. Although more rigorous monitoring may come at an increased cost, the benefits of installing mitigation measures that are proven to work will be more cost effective in the long term. Collaboration between ecological and environmental consultants and practicing scientists may not only help to develop the most effective protocols and analysis methods, but integrated projects between agencies and universities may also allow pooling of resources and will encourage scientific research to feed into the evidence base required for conservation. For example, through our work funded by Defra, we aim to use the methodologies we have developed to further quantify the population/landscape scale effects, of both roads and rail, on bats in a variety of situations (e.g. different road classes, traffic flows, habitats and geographical locations) and to further assess the success and cost effectiveness of currently used mitigation measures. Our goal is to provide a robust standardised working protocol that may be applied by conservation practitioners and the consultancy industry and practical guidelines based on evidence to inform successful future mitigation.

Although our focus is on bats and roads, the issues and recommendations discussed can be applied to the conservation of other wildlife and mitigation studies in general. Crossing structures over or under roads such as bridges and underpasses have become a worldwide mitigation tool for a whole range of wildlife, including large mammals (e.g. Olsson *et al.* 2008; Kusak *et al.* 2009), small mammals (e.g. Clevenger *et al.* 2001; Soanes *et al.* 2013), and amphibians and reptiles (e.g. Ng *et al.* 2004; Aresco 2005). However, there is little or no evidence for their effectiveness at the population level, or even at the level of assessment as a safe crossing point for a significant proportion of animals. Poor experimental design, a lack of rigorous evaluation and the subjective nature of current practice have been highlighted for mitigation for all wildlife, both in the UK (Byron *et al.* 2000) and in other parts of the world e.g. Europe (Roedenbeck *et al.* 2007), North America (Forman *et al.* 2003) and Australia (Van der Ree *et al.* 2007). Problems such as poor implementation and insufficient monitoring have also led to a lack of evidence for the effectiveness of habitat compensation measures (e.g. Tischew *et al.* 2010). Crossing structures and habitat compensation may be useful mitigation measures for many species of wildlife in a range of situations, but it is important that the effectiveness of such measures are assessed reliably, ideally at the population level before they are accepted into conservation practice. Robust and effective methods, such as those used and recommended in this study, may be modified to monitor other wildlife species or mitigation structures, and such methods should be adopted in ecological consultancy. This approach is also not just applicable to roads, but to conservation as a whole, which urgently requires a shift towards evidence-led practices rather than those based predominantly on expertise (see section 6.4).

6.3 Future recommendations for bats and roads

(i) Wire bat gantries (of the design we studied) should not be built and attempts to divert bats should be avoided

(ii) Further research should focus on crossing structures built on original bat commuting routes, such as underpasses and green bridges

(iii) Unique aspects of individual sites, such as tree cover, hedges and topography must be exploited to make mitigation solutions as natural as possible, appropriate to the bat species present and cost effective

(iv) We suggest an integrated approach to mitigation combining several measures, such as crossing structures and habitat improvements, that address the different negative impacts of roads on bats

(v) Robust pre- and post-construction monitoring using a standardised methodology (such as in this study) should be applied to assess the effectiveness of future mitigation schemes and build an evidence base to inform effective conservation practices.

6.4 The importance of evidence-based conservation

This study has provided an ideal model to demonstrate the need for greater use of evidence in practical conservation. Considerable sums of money are spent on mitigation measures that have not been proven to work. For example, numerous wire bat gantries have been built in the UK in recent years at huge cost, and we now have evidence that they are ineffective. Not only is this a financial waste, but it may result in irreversible damage to bat populations that are not being protected effectively. It is important that an evidence-base is built upon to include a range of scenarios and species to allow informed decisions to be made for effective mitigation and successful conservation. This lack of quantitative evidence does not just apply to bat conservation, but is common for all types of wildlife. Conservation decisions are frequently based on anecdotal sources such as personal experience and common sense, and rarely on verifiable scientific evidence (Pullin *et al.* 2004; Sutherland *et al.* 2004; Cook *et al.* 2010), which is both lacking and often inaccessible to practitioners (Fazey *et al.* 2005). The consequences of conservation actions are also rarely documented, and there is no framework upon which knowledge can develop. Experience-based solutions may not always be inadequate, but can result in the adoption of conservation practices based on myth or incorrect information, with inappropriate and ineffective solutions, as demonstrated in this study. Some other examples include: the winter flooding of grassland which is widely encouraged to benefit wading birds has been found to kill the invertebrates upon which the birds feed (Ausden *et al.* 2001), a systematic review of the effectiveness of engineered in-stream structures widely used to increase salmonid abundance found the available evidence to be equivocal (Stewart *et al.* 2009), and a method to monitor tiger populations in India was found to be ineffective despite being used by wildlife managers for thirty years (Karanth *et al.* 2003).

There has been a revolution in medical practice and public health over the last few decades, with a shift from expert experience and opinion to an evidence-based practice (Stevens & Milne 1997). This has been achieved through the development of an online database of systematic reviews, and wide dissemination to incorporate medical research into medical practice, and such changes have been suggested for conservation practice (Pullin & Knight 2003; Sutherland *et al.* 2004). Parallels have been drawn between medical practice and conservation biology, in that they both require effective quick solutions often involving ethical and moral decisions, with a similar relationship between academics and practitioners (Pullin & Knight 2001). Although this change would require a significant shift in the way conservation practice operates, the medical health care model shows that it can be achieved. Conservation organisations have also recognised the need to make greater use of evidence in their practices, and would be likely to support such changes (Sutherland *et al.* 2004). Not only would this speed up decision making and lead to more effective conservation, but the ability to demonstrate the effectiveness of conservation measures may also strengthen the case for investment in conservation by funders and policy formers (Sutherland *et al.* 2004; Ferraro & Pattanayak 2006). One of the major problems faced by practitioners is the accessibility of evidence from the scientific literature, and the time it takes to locate and review this evidence (Fazey *et al.* 2005; Pullin & Knight 2005). To be successful, an evidence-base must therefore be readily accessible and appropriate to the questions that decision makers need answers to. The journal Conservation Evidence, established in 2004, has set up an online database providing an authoritative source of information, summarising evidence for conservation interventions (www.conservationevidence.com). The project aims to produce synopses of summaries for interventions for every major habitat and taxonomic group. Current synopses cover bees (Dicks *et al.* 2010), birds (Williams *et al.* 2013), farmland (Dicks *et al.* 2013), bats (Berthinussen *et al.* 2013) and many others are in production. Although evidence is lacking for many common conservation interventions (Sutherland *et al.* 2013), this provides a framework upon which an evidence-base can be built through both scientific research and the work of conservation practitioners. These kinds of changes are urgently needed to close the gap between science and conservation practice and improve the effectiveness and efficiency of wildlife conservation.

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